AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2791, pp. 1–35, figs. 1–21 August 13, 1984

A Morphometric Analysis of *Carollia* (Chiroptera, Phyllostomidae)

LAURA JOHN MCLELLAN[1]

CONTENTS

Introduction 2
Methods and Materials 4
Acknowledgments 9
Variation among *Carollia* Species. 9
Patterns of Variation within Species 11
Sexual Dimorphism 13
Locality Trends 15
Phenetic Relationships among Populations 25
Discussion and Conclusions 26
Literature Cited 33

ABSTRACT

The species of bats in the genus *Carollia* present a complex pattern of morphological variation which complicates identification of species. I examined sexual and geographic variation in cranial and mandibular measurements of 475 specimens of *Carollia* selected to represent the geographic range of each species in the genus: *brevicauda, castanea, perspicillata,* and *subrufa.* All species were easily separated by canonical variates analysis, with *C. castanea* being the most distinctive. Sexual dimorphism is present in all species and males consistently are larger than females. Significant differences are present among populations in all species. *Carollia subrufa* and *C. brevicauda* have morphologically distinct populations in the northern and southern portions of their range, whereas different populations of *C. castanea* sampled show no clear geographic pattern. Character values from samples of *C. perspicillata* form a continuum with non-overlapping values from the northernmost and southernmost portions of their geographic range.

[1] Curatorial Intern, Department of Mammalogy, American Museum of Natural History.

Copyright © American Museum of Natural History 1984

ISSN 0003-0082 / Price $3.40

INTRODUCTION

Bats of the genus *Carollia* (family Phyllostomidae) are among the most common mammals in tropical American faunas. They range from northern Mexico to Paraguay and live in most habitats, except those at elevations higher than 2150 m, and in very arid regions. In spite of the many specimens of *Carollia* in museum collections, taxonomy of this genus has been confused, largely owing to the difficulty of accurately delimiting species, as reflected in the nomenclatural history of the genus.

Linnaeus (1758) first described a *Carollia* under the name *Vespertilio perspicillatus.* In part because of the ambiguity of his description, considerable nomenclatural confusion existed for members of the genus *Carollia* until 1907 when Hahn (1907) produced the first revision of the genus. He recognized three species under the generic name *Hemiderma*: *H. perspicillatum* with two subspecies *perspicillatum* and *aztecum, H. subrufum* Hahn, and *H. castaneum* H. Allan. At that time only 374 specimens were available for Hahn to study and these poorly represented the distributional range of the genus. In 1924, Miller resurrected the generic name *Carollia* (previously considered a junior homonym of the fossil pelecypod *Carolia*). *Carollia subrufum* and *C. castaneum* were considered conspecific by Felten (1956) who, following Elliot (1904) presented a key based on measurements to separate the two species (*C. perspicillata* and *C. castanea*) that he recognized. Subsequently, there was a fair amount of confusion over the number of species of *Carollia.* It proved particularly difficult to find distinguishing characters that consistently separated species over their entire range. Hall and Kelson (1959; species *C. perspicillata* and *C. castanea* recognized) noted that individuals of each species were larger from the northern part of their geographic range than those from the southern part. At that time they were unable to make a key that could distinguish the species they recognized from one another at all locations.

Pine (1972) presented a revision of the genus where he recognized four species, describing and adding *C. brevicauda* to the list of widely accepted species. He used classical methods in his revision of the genus, examining a large number of specimens from throughout the range of each species, in search of distinguishing characters. He was able to find a combination of characters to distinguish four species. These characters include cranial features, tooth morphology, body size, and pigment distribution in hair shafts. Pine provided a key to the species that is useful when both skins and cleaned skulls are available and when the specimens are from the same geographic region. Although Pine's classical approach has proved useful at the species level, intraspecific variation among populations has not been clearly described. Pine noted that intraspecific variation existed within the species of *Carollia,* but he did not quantify this variation. Two intraspecific size trends noted by Pine are: (1) individuals from northern populations were larger than those from the south in all species except *C. castanea* and (2) male *C. perspicillata* tend to be larger than females. He further noted that specimens of *Carollia* from sympatric populations were more easily identified to species than were specimens from allopatric populations of the same species. Pine (1972, pp. 4, 27, 76) treated *C. perspicillata* as polytypic and suggested that *C. subrufa* may have recognizable subspecies.

Hall (1981), in his most recent treatment of North American mammals, follows Pine (1972) in his key to the species of *Carollia.* The key is still difficult to use to differentiate between *C. brevicauda* and *C. perspicillata.* Koopman (1978) notes that the skull characters Pine describes are subtle and difficult to use to distinguish between *C. brevicauda* and *C. perspicillata* from Peru. Even Pine notes character convergence in samples of *C. brevicauda* from Panama (with *C. subrufa*), and in *C. perspicillata* sampled from Paraguay (with *C. brevicauda*).

I re-examined specimens of *Carollia* assigned to species by Pine (1972) to describe character variation within the four species. Morphometric techniques were used on cranial and mandibular measurements to evaluate individual, sexual, interpopulational and interspecific variation. I examined the following points:

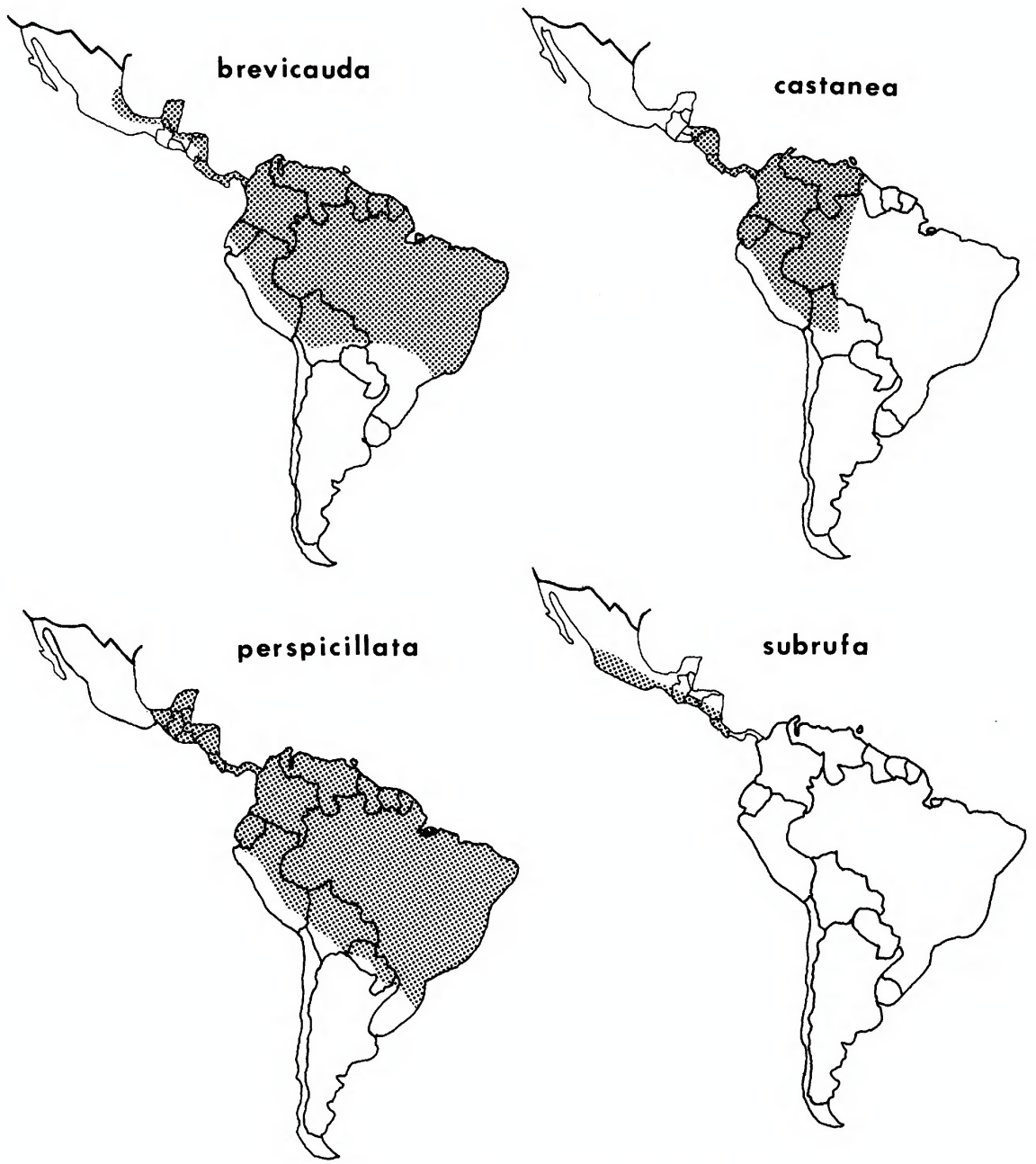

FIG. 1. Geographic distribution of species in *Carollia*.

1. How distinctive, in a quantitative sense, are the four nominate species recognized by Pine?
2. How is the variation due to individuals, sex, and location apportioned?
3. How do the individual species vary between sexes and among populations?
4. Are the kinds and magnitude of variation within each species concordant among species?

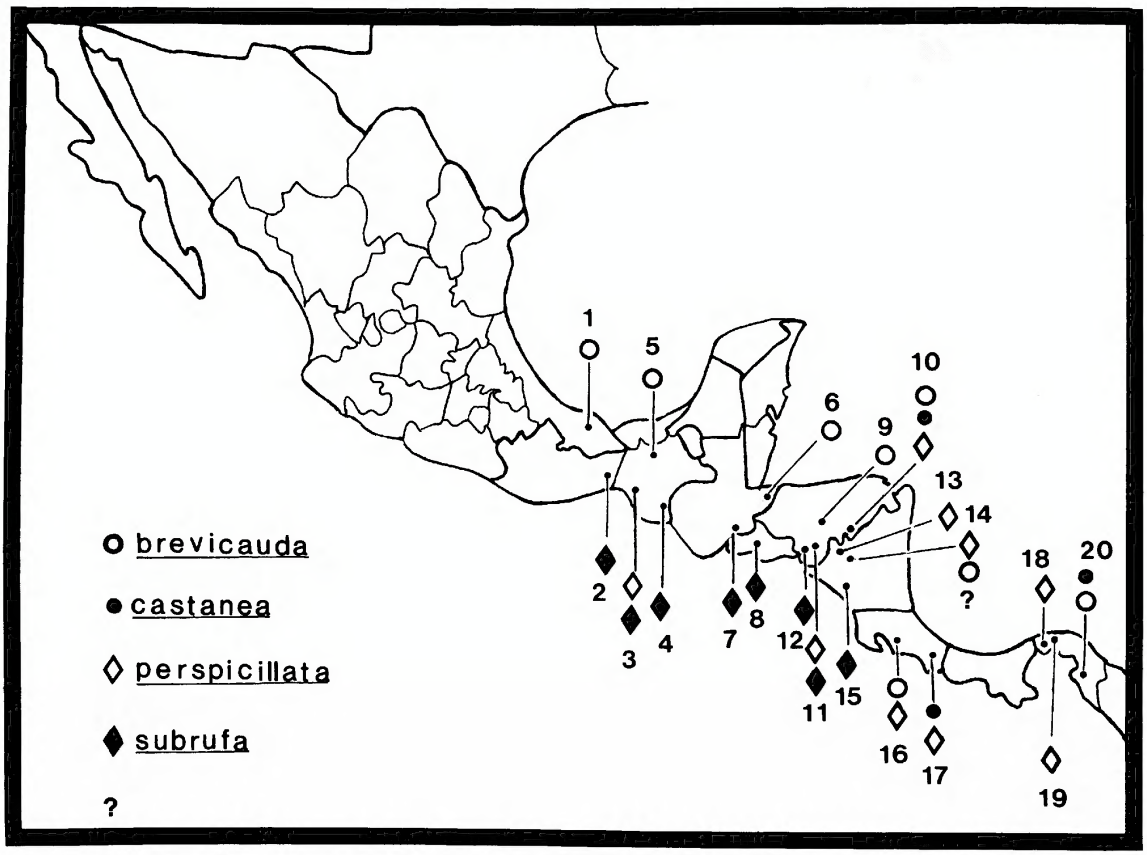

FIG. 2. Population samples examined from Mexican and Central American localities. Numbers correspond to localities listed in specimens examined. Vertical lists of symbols indicate sympatric populations of several species. Question marks represent those specimens that Pine (1972) was unable to identify to species.

5. What are the phenetic relationships of the populations within and among species?

This analysis extends Pine's study—using only specimens which he examined for his monograph—to describe the patterns of geographic, sexual, and individual variation within the species of *Carollia*. The characters selected and the statistical techniques applied provide a different view of some of the same samples of *Carollia* examined by Pine (1972). Multivariate methods are used here in both a confirmatory and investigative manner, first to test Pine's observations and then to further examine intraspecific variation within the species of *Carollia*. Comparisons of individual, sexual and geographic patterns of variability in the species of *Carollia* are made and hypotheses concerning factors responsible are addressed.

METHODS AND MATERIALS

STATISTICAL ANALYSES: I examined 475 male and female skulls of *Carollia* from locations selected to represent the distributional range of the genus (fig. 1). All the specimens were examined previously by Pine (1972) in his study. I used only specimens judged adult by Pine (1972), based on fusion of the epiphyses of the metacarpals and phalanges. Only samples from Pine's study with more than two individuals were included in the analysis. Thirteen was the average number of individuals examined per population. Specimens of *C. castanea* (n = 64) were ex-

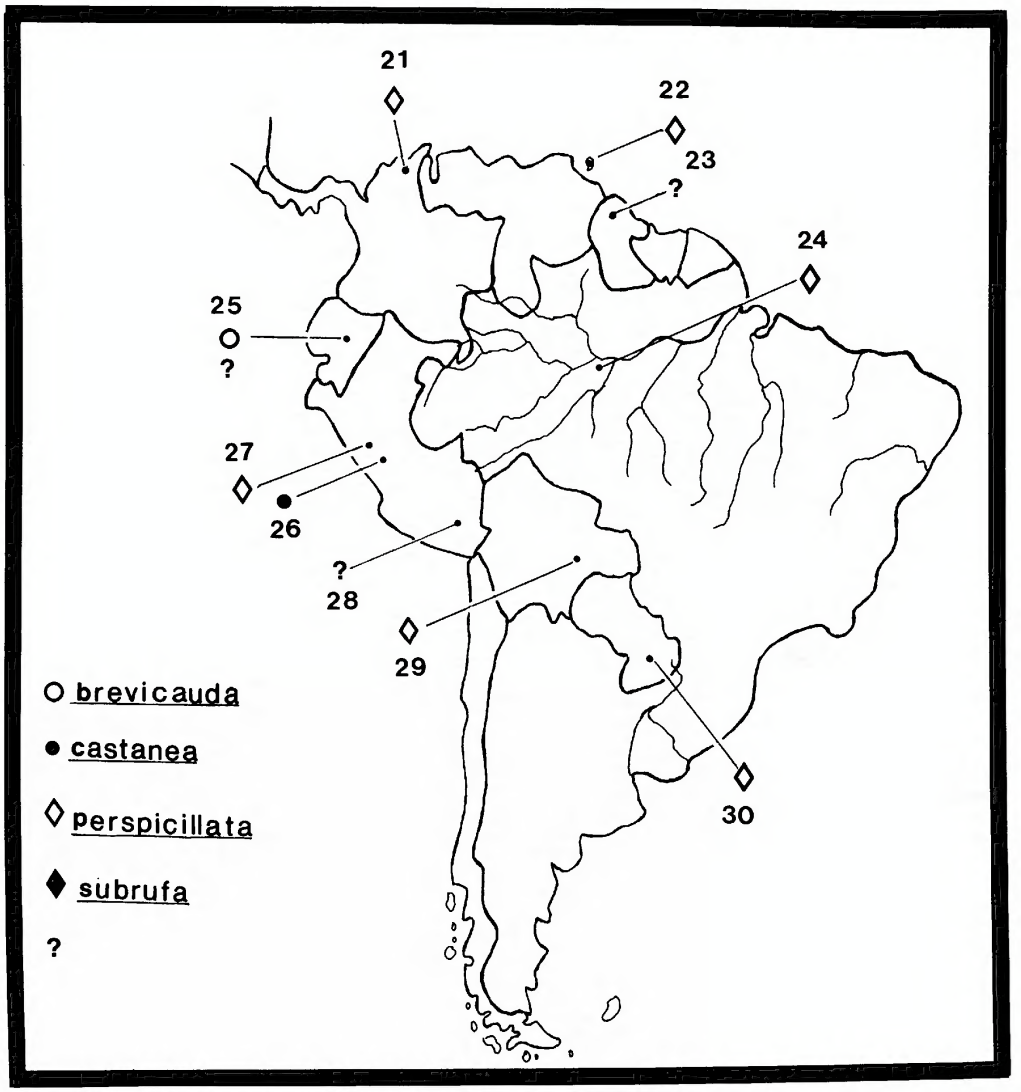

FIG. 3. Population samples examined from South American localities. Numbers correspond to localities listed in specimens examined. Vertical lists of symbols indicate sympatric populations. Question marks represent those specimens that Pine (1972) was unable to identify to species.

amined from four localities extending from Honduras to Peru. *Carollia subrufa* (n = 73) was examined from eight localities along the Pacific versant of Central America from Mexico to Nicaragua. Nine populations of *C. brevicauda* (n = 123) are represented, ranging from Mexico to Ecuador. *Carollia perspicillata* (n =215) is the best represented species with specimens examined from 15 localities, ranging from Mexico to Paraguay (figs. 2 and 3). Pine left four specimens unclassified to species. These individuals were from separate localities in Nicaragua, British Guiana, Ecuador, and Peru. They were included in certain of the analyses to more accurately determine their phenetic relationships.

Twenty-two cranial and mandibular characters were measured (fig. 4). Linear measurements were taken to the nearest 0.1 mm using dial calipers and one angular measurement was taken using a goniometer mounted on a dissecting microscope. In order to mea-

sure the slope of the forehead, the skull was set on its side in a clay block on top of a piece of graph paper. The upper edge of the maxillary toothrow was aligned with a line on the graph paper and used as a base line. The crosshair of the goniometer was aligned perpendicular to the toothrow and passing through the inflection point between the cranium and the rostrum. The angular measure was taken between this perpendicular crosshair and the forehead. Linear characters include: basilar length (BAL), palatar length (PL), postglenoid width (PGW), breadth of braincase (BB), depth of braincase (DB), least interorbital breadth (LIB), rostral breadth (RB), length of maxillary spur (MSL), length of maxillary toothrow (MTR), width between first molars (MW), width between second premolars (PMW), width between canines (CW), dorsal rostral length (DRL), ventral rostral length (VRL), palatal width (PW), foramen magnum width (FMW), mandibular length (ML), mandibular depth (MD), coronoid-angular distance (CAD), height of coronoid (CH), and postdentary ramus length (PDRL).

Statistical analysis of the data was performed at Michigan State University using the Statistical Package for the Social Sciences (SPSS; Nei et al., 1975) and Clustan (Cluster Analysis Package; Wishart, 1978). The mean squares for differences due to species and due to populations and sexes within species are calculated in two separate nested one-way analyses of variance using SPSS MANOVA; from these the magnitude of the respective variance components are estimated. The variance components themselves are not comparable over characters or taxa because of varying sample sizes and unequal variances, but the magnitude relative to the total variance within each character can be compared. The relative magnitude of these variance components was used to determine the importance of sources of variation (Straney, 1978; Leamy, 1983).

Characters that vary across localities were examined for latitudinal trends by correlating sample character means with geographic coordinates for each species. Significant differences between character means of the populations within each species were determined using a one-way analysis of variance and Scheffe's multiple range test ($P = 0.05$). A univariate F test was used for testing for differences between characters for the sexes within each species.

Discriminant analysis was used to assess the distinctiveness of species, populations within species and the sexes within species. Classical discriminant analysis produces a linear function of the characters for each group yielding scores that can be used to assign unknown specimens to *a priori* groups. Closely related to discriminant function analysis is canonical variates analysis, both of which were obtained from the same program, SPSS DISCRIMINANT. Canonical variates analysis maximally separates *a priori* groups by maximizing the *among group* variance relative to the *within group* variance of the characters used in the analysis. This is accomplished by giving characters that vary according to group (species, population, or sex) high weightings and those that vary independently low weightings. This procedure corrects for correlated characters and adjusts for differing covariance between groups compared. The first canonical variates axis always explains the greatest amount of the character variance between groups. The second axis explains the next greatest amount of variance of an axis orthogonal to the first axis and so on for each additional axis. On each axis, the individual characters are given a value (standardized canonical variates coefficient) which corresponds to their importance in separating groups; the larger the absolute value, the more important the character.

Mahalanobis distance was used to place the four unknown specimens (left by Pine, 1972) to species. Mahalanobis distance is the Euclidean distance squared in the 3 dimensional space defined by the canonical variates. Each specimen is assigned to the species sample with the closest group centroid (mean character vector).

The relationship among populations is summarized using cluster analysis (unweighted pair group method). This analysis produces a dendrogram that graphically represents similarity among populations in a branching diagram. The squared Euclidean distance between population centroids is used to calculate the similarity matrix. Populations of all species are entered together.

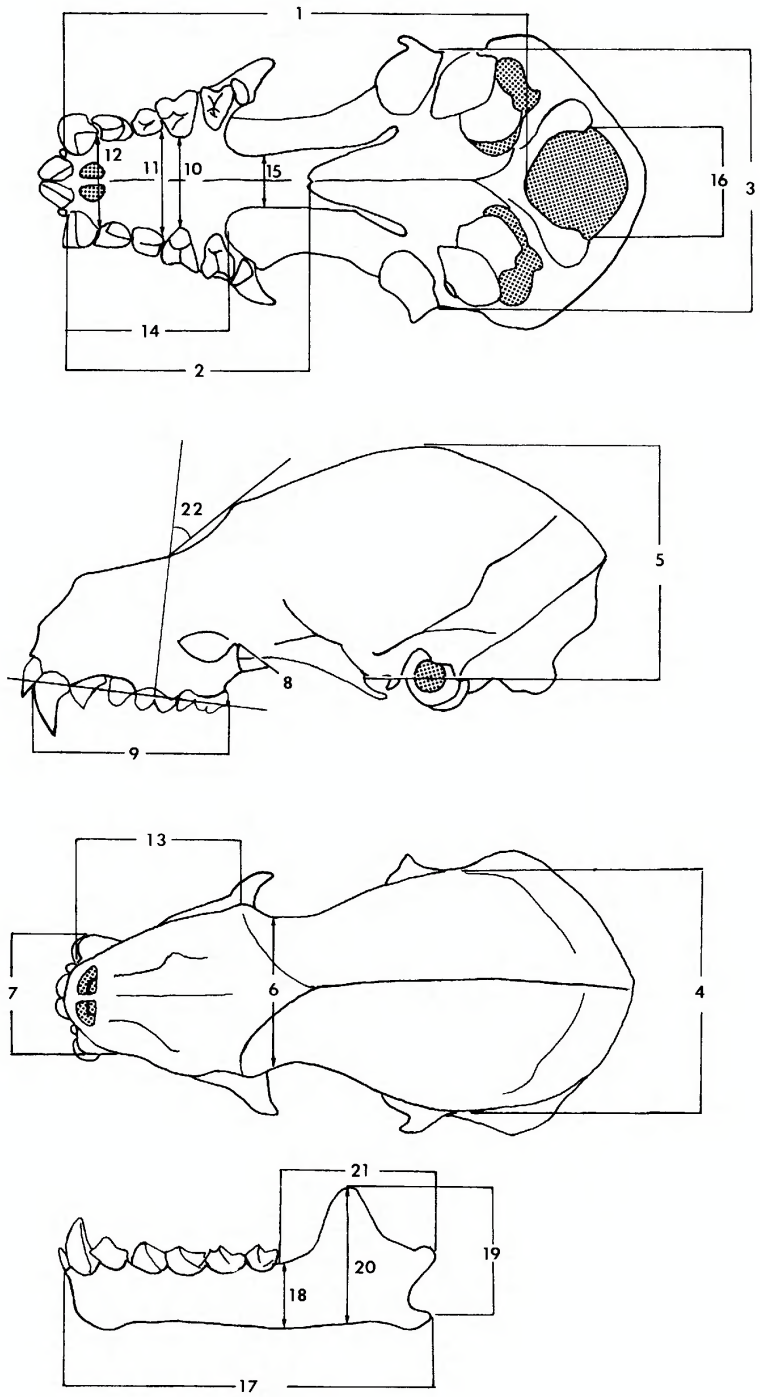

FIG. 4. *Carollia* skull and mandibular ramus indicating measurements used in study. Abbreviations indicated in parentheses. 1. Basilar length (BAL); 2. Palatar length (PL); 3. Postglenoid width (PGW); 4. Breadth of braincase (BB); 5. Depth of braincase (DB); 6. Least interorbital breadth (LIB); 7. Rostral breadth (RB); 8. Maxillary spur length (MSL); 9. Maxillary toothrow (MTR); 10. Width between first molars (MW); 11. Width between second premolars (PMW); 12. Width between canines (CW); 13. Dorsal rostral length (DRL); 14. Ventral rostral length (VRL); 15. Palatar width (PW); 16. Foramen magnum width (FMW); 17. Mandibular length (ML); 18. Mandibular depth (MD); 19. Coronoid angular distance (CAD); 20. Coronoid height (CH); 21. Postdentary ramus length (PDRL); 22. Slope of forehead (SF).

SPECIMENS EXAMINED: The collecting localities are grouped below according to species. Specific localities from which specimens were examined are grouped by country. Museum acronyms are: AMNH—American Museum of Natural History; CM—Carnegie Museum; FMNH—Field Museum of Natural History; KU—University of Kansas Museum of Natural History; LACM—Los Angeles County Museum; TCWC—Texas Cooperative Wildlife Collection; USNM—United States National Museum, Smithsonian Institution. Numbers in parentheses following town represent map locations indicated in figures 2 and 3.

Carollia brevicauda

MEXICO—Veracruz: Rio Quezalapam (1), 2 mi E Lago Catemaco, 5♂♂, 7♀♀ (TCWC 11131–11137, 11140, 11142–11145); Chiapas, 21 km WSW Teapa (Tabasco) in Chiapas (5), 200 ft, 3♂♂, 4♀♀ (TCWC 16502, 16504–16509). GUATEMALA: Izabal (6), 25 km WSS Puerto Barrios, 300 ft, 15♂♂, 10♀♀ (TCWC 17295–17319). HONDURAS: Francisco Morazan (9), 10 mi NE Talanga, 3400 ft, 1♂, 1♀ (TCWC 10844–10845); Rio Coco (10), 78 mi ENE Danli, 900 ft, 1 sex?, 3♂♂, 8 ♀♀ (TCWC 9893, 9898, 9901, 9907, 9913–9918, 10654–10655). NICARAGUA: Dept. Madriz Yalaguina (14), 10 km E Somoto, 2200 ft, 5♂♂, 1♀ (TCWC 8873, 8888–8889, 8900–8902). 1 km SE Yalaguina (14) 2600 ft, ♀ (TCWC 7414–specimen Pine (1972) was unable to assign to species). COSTA RICA: Alajuela Cariblanco (16), 18 mi NE Naranjo, 3000 ft, 1♂, 2♀♀ (TCWC 9867, 9872, 9876). PANAMA: Tacarcuna Village Camp (20), 3200 ft, 18♂♂, 24♀♀ (USNM 309474–309479, 309481–309497, 309499–309509, 309516–309526). ECUADOR: Napo Pastaza (25), 8 mi WNW Puyo, 3800 ft, 9♂♂, 7♀♀ (TCWC 12047–12051, 12054, 12056–12057, 12059–12062, 12064–12067) (TCWC 12068–specimen Pine (1972) was unable to assign to species).

Carollia castanea

HONDURAS: Rio Coco (10), 78 mi ENE Danli, 900 ft, 8♂♂, 3♀♀ (TCWC 9935–9945). COSTA RICA: Puntarenas Prov. (17), 4 mi NE Palmar, 300 ft, 2♂♂, 6 ♀♀ (TCWC 9919–9926). PANAMA: Darien, Tacarcuna Village Camp (20), 1850 ft, 28♂♂, 13♀♀ (USNM 309406–309411, 309413–309420, 309423, 309425–309431, 309433–309438, 309441, 309443–309449, 309453–309456). PERU: Huanuco (26), 19 mi S Tingo Maria, 2800 ft, 3♂♂, 2♀♀ (TCWC 11915–11919).

Carollia perspicillata

MEXICO—Chiapas: 21 km WSW Teapa (Tabasco) (5), 200 ft, 5♂♂, 6♀♀ (TCWC 16435–16439, 16441–16446). HONDURAS: Francisco Morazan, 2 mi SE Sabana Grande (11), 1♂, 1♀ (TCWC 10856–10857); Rio Coco (10), 78 mi ENE Danli, 900 ft, 4♂♂, 14♀♀ (TCWC 9889, 9891–9892, 9894–9897, 9899–9900, 9902–9906, 9908–9911). NICARAGUA: Dept. Madriz Yalaguina (13), 10 mi E Somoto, 2200 ft, 1♂, 1♀ (TCWC 8874–8875); Dept. Chontales, 1 km NW La Gatiada (14), 1300 ft, 4♂♂, 6♀♀ (TCWC 8860–8865, 8867–8870). COSTA RICA: Alajuela Cariblanco (16), 18 mi NE Naranjo, 2900–3000 ft, 4♂♂, 3♀♀ (TCWC 9864, 9866, 9868–9871, 9873); Prov. de Puntarenas (17), 4 mi NE Palmar, 300 ft, 6♂♂, 12♀♀ (TCWC 9845–9848, 9850, 9852–9863). PANAMA: Bat Caves, Madden Dam Rd. (19), 10♂♂, 5♀♀ (LACM 20075, 20079–20093); R de Panama (18), 18 km WSW Chepo, 200 ft, 7♂♂, 6♀♀ (TCWC 11920–11921, 11923, 11926–11929, 11937–11940, 11942–11943). COLOMBIA: Magdalena Sierra Negra (21), Villanueva Valledupar, 7♂♂, 4♀♀, 1 sex? (USNM 281106–281115, 281121–281122). TRINIDAD: San Rafael (22), 2♂♂, 2♀♀ (FMNH 61926–61929). BRAZIL: Rio Madeira Rosarinho (24), 26♂♂, 26♀♀ (AMNH 92056–92061, 92063–92070, 92072–92078, 92080–92100, 92182–92187, 92220, 92627, 92629, 92632, 92634). PERU: Loreto (27), 11 mi SE Pucallpa, 300 ft, 500 ft, 5♂♂, 15♀♀ (TCWC 11982–11983, 11985–12002). Puno, Sandia Prov. San Juan, Tanbopata Valley (28), 5000 ft, ♂ (FMNH—specimen Pine was unable to assign to species). BOLIVIA: Dept. Santa Cruz, Prov. de Sara, Buenavista (29), 400 m, 450 m, 500 m, 10♂♂, 4♀♀ (LACM 8942; FMNH 22442, 22444–22447; CM 2163, 2200; AMNH 61755–61760). PARAGUAY: Sapucay (30), 1♂, 13♀♀ (FMNH 18208–18209); USNM 114005—the holotype of *C. p. tricolor,* 115003–115012).

Carollia subrufa

MEXICO—Oaxaca: 4 mi E Tapanatepec (2), 800 ft, 4♂♂, 8♀♀ (TCWC 16449–16450, 16452–16455, 16458–16560). Chiapas: 5 mi N Arriaga (3), 800 ft, 7♂♂, 10♀♀ (TCWC 16478–16494); 4 km NW Tapachula (4), 450 ft, 7♂♂, 12♀♀ (TCWC 14276–14284, 14499–14508). GUATEMALA: Chiquimula (1), 20 km SSE Chiquimula, 550 m, 3♂♂, 7♀♀ (TCWC 17269–17278). HONDURAS: Valle (10), 10 km E San Lorenzo, 25 ft, 4♂♂, 2♀♀ (TCWC 18353–18359); Francisco Morazan, 3 mi S Sabana Grande (11), 1500 ft, 1♂, 1♀ (TCWC 10846, 10859). EL SALVADOR: La Libertad (8), 20 mi W La Libertad, 3♂♂, 1♀ (TCWC 8903–8905, 9807). NICARAGUA: Chinandega (15), San Antonio, 15 mi, 2♂♂, 4♀♀ (KU 97660–97665). British

Guiana (Guyana) Kartabo ♀ (AMNH 64168—specimens Pine was unable to assign to species).

ACKNOWLEDGMENTS

Originally, the present report was completed to satisfy partial requirements for the degree of Master of Science in Biology in the Graduate School, Michigan State University in September 1983. I am most grateful to Dr. Donald O. Straney, my official graduate student advisor, for his patience and guidance. Drs. T. Wayne Porter and Charles Cress, both members of my thesis committee, provided wise counsel. I thank Drs. Ronald H. Pine, Karl F. Koopman, Sydney Anderson, and Guy G. Musser for carefully reading the manuscript and providing critical reviews; Dr. Musser encouraged me to revise the manuscript and follow it through to publication. Dr. Hugh Genoways, Dr. Karl F. Koopman, Ms. Sheila Kortlucke, Dr. Donald Patton, Dr. James D. Schmidly, Mr. Robert Fisher, and Dr. Robert Timm permitted me access to specimens under their care; I appreciate their help. Financial support was supplied by The Museum and Department of Zoology, Michigan State University.

VARIATION AMONG *CAROLLIA* SPECIES

Relative proportions of variation among and within species for each of the 22 characters examined are listed in table 1. Characters with large variance components attributed to species differences are potentially useful discriminating characters. Differences among species account for only 57.5 percent of the average character variance leaving on average 42.5 percent of the variance attributable to within-species differences. The best distinguishing characters appear to be basilar length, maxillary toothrow length, ventral rostral length, coronoid-angular distance, mandibular length, and coronoid height. Each of these differs significantly among species, determined by a one-way analysis of variance and Scheffe's multiple range test. For each of these characters, the mean measurement is greatest for *C. perspicillata* followed in decreasing order by *C. brevicauda, C. subrufa,* and *C. castanea* (table 2).

There are six characters that vary more within species than among species. They are least interorbital width, maxillary spur length, distance between the first molars, foramen magnum width, mandibular depth and slope of forehead. These characters vary in accordance with other factors.

TABLE 1
Percentage of Total Variation Attributable to Species Differences[a]

Variable	% Variation		
	Between Species	Within Species	Total Variance
Basilar length	78.4	21.6	150.18
Palatar length	58.8	41.2	42.57
Postglenoid width	63.2	36.8	21.03
Breadth of braincase	56.7	43.4	12.42
Depth of braincase	60.9	39.1	20.45
Least interorbital breadth	18.6	81.4	3.85
Rostral breadth	55.5	44.5	7.50
Maxillary spur length	36.5	63.5	7.45
Maxillary toothrow	82.8	17.2	36.73
Width between first molars	43.4	56.6	6.94
Width between second premolars	71.1	28.3	17.98
Width between canines	60.9	39.1	7.08
Dorsal rostral length	64.8	35.2	25.84
Ventral rostral length	79.4	20.6	27.11
Palatal width	57.1	42.9	3.50
Foramen magnum width	15.8	84.2	3.65
Mandibular length	78.3	21.7	95.64
Mandibular depth	40.2	59.8	6.01
Coronoid angular distance	79.1	20.9	42.29
Coronoid height	78.3	21.7	38.88
Postdentary ramus length	72.3	27.7	31.08
Slope of forehead	11.4	88.6	11.47
Mean	57.48	42.55	

[a] Total variation is the character variance over all species.

The four species of *Carollia* described by Pine (1972) were easily separated in canonical variates analysis (fig. 5) using all 22 characters. Over all species, 98.67 percent of the specimens were correctly assigned to species using three canonical axes. *Carollia castanea* is the most distinctive, with 100 percent of the specimens correctly classified to species

TABLE 2
Mean Character Values (mm ± 2 Sx̄) from *Carollia* Useful in Species Discrimination[a]

	C. perspicillata	*C. brevicauda*	*C. subrufa*	*C. castanea*
BAL	181.1 ± 0.86	176.5 ± 0.95	167.3 ± 0.99	155.2 ± 0.97
MTR	75.3 ± 0.42	69.5 ± 0.43	67.3 ± 0.39	62.8 ± 0.40
VRL	63.0 ± 0.38	58.8 ± 0.42	56.7 ± 0.36	51.3 ± 0.39
CAD	57.0 ± 0.51	53.9 ± 0.45	50.8 ± 0.47	43.0 ± 0.45
ML	144.1 ± 0.76	138.5 ± 0.80	133.9 ± 0.62	123.3 ± 0.75
CH	51.5 ± 0.50	48.0 ± 0.43	44.5 ± 0.36	38.3 ± 0.55

[a] For abbreviations see legend of figure 4.

(using SPSS-DISCRIMINANT). Individuals of *C. subrufa* group tightly with 100 percent of the specimens correctly classified. *Carollia subrufa* falls closer (using Mahalanobis distance) to *C. brevicauda* and *C. perspicillata* than to *C. castanea. Carollia brevicauda* and *C. perspicillata* overlap slightly with 3.4 percent of the *C. brevicauda* classified as *C. perspicillata* and 1 percent of the *C. perspicillata* classified as *C. brevicauda.*

Species are maximally separated along the first canonical variates axis with *C. subrufa* and *C. brevicauda* falling between *C. castanea* and *C. perspicillata.* Characters with high loadings on this axis are maxillary toothrow (−0.56), width between first molars (0.42) and palatar length (0.49). The second canonical axis separates *C. brevicauda* from the rest of the species. Characters important here are basilar length (1.14), maxillary toothrow (1.77), and postdentary ramus length (0.49). The third axis separates *C. subrufa, C. castanea,* and *C. brevicauda.* Important in this separation are maxillary toothrow (−1.12) and maxillary spur length (−0.66). Maxillary toothrow is consistently important in species separation. The nature of some of these variables (palatar length, maxillary toothrow length and basilar length) suggests that skull length is a major factor in separation of species using canonical variates analysis.

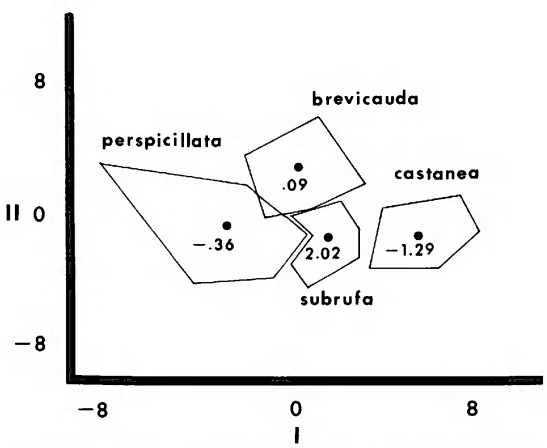

FIG. 5. Canonical variates analysis of *Carollia.* Each species is represented by a tracing of the perimeter of the cluster formed by individual specimens included in the analysis. Group centroid for each species is represented by a solid dot. The x and y axes are the first and second canonical axes, respectively; the third axis value is printed below the group centroid. Units of these axes represent the canonical variates scores. Areas of overlap represent specimens which fall into species groups other than the *a priori* assigned group.

Size appears to be an important factor in discriminating among *Carollia* species. The first canonical axis accounts for 71.59 percent of the total variation among species. Low values correspond with the largest individuals in the study (specimens of *C. perspicillata*), whereas the high values are associated with the smallest specimens (*C. castanea*). Specimens of *C. subrufa* and *C. brevicauda* are not separated on the first axis, but are on the second. The second axis separates *C. brevicauda* and *C. subrufa* from each other and the third axis fully separates *C. subrufa, C. brevicauda,* and *C. perspicillata.*

The specimens left unidentified by Pine (1972) were classified to species using discriminant analysis. Unknowns were placed to the species with the nearest group centroid (least Mahalanobis distance). The specimens from Yalaguina, Nicaragua and Napo Pastaza, Ecuador were placed with *C. brevicauda.* The specimen from Kartabo, British Guiana was placed with *C. subrufa* and the

TABLE 3
Percentage Contribution to Total Variance of Locality, Sex and Residual for Each Species of *Carollia*[a]

Species	Locality	Sex	Residual	Total
C. castanea	29.25	4.07	66.68	116.64
C. subrufa	16.02	6.10	77.88	88.36
C. brevicauda	20.18	6.86	72.96	163.53
C. perspicillata	34.60	6.83	58.57	271.23
Mean	25.01	5.97	69.02	

[a] Values are averaged over 22 characters.

specimen from San Juan, Peru was placed with *C. perspicillata*. All four of these specimens fell close to the region where individuals of *C. subrufa, C. brevicauda,* and *C. perspicillata* come into close proximity in canonical variates space.

PATTERNS OF VARIATION WITHIN SPECIES

The relative importance of the sources of variation within species was examined in a two-level nested analysis of variance estimating variance components due to: (1) differences between localities; (2) differences between sexes within localities, and (3) residual variation. Expressed as a percentage of the total variation within each species and averaged over 22 characters, most of the variation is residual (58.6–77.9%) and between localities (16.0–29.3%) in all four species (table 3). The contribution due to sex is the smallest source of variation examined (4.1–6.9%) in agreement with the results of Leamy (1983) using laboratory mice and Straney (1978) using ocelots, skunks, and wild mice to measure variance components.

The pattern of character variation within each species varies among species (figs. 6–9). All *Carollia* have a large locality component in basilar and ventral rostral lengths (>30%). Both *C. castanea* and *C. perspicillata* have locality effects in all 22 characters. Rostral breadth is sexually dimorphic in all four species. The distribution of variance components due to sex are similar in *C. subrufa* and *C. brevicauda*. Both have characters with large sex components independent of locality effects. Three of these characters are common to both species including depth of braincase, rostral breadth, and mandibular depth.

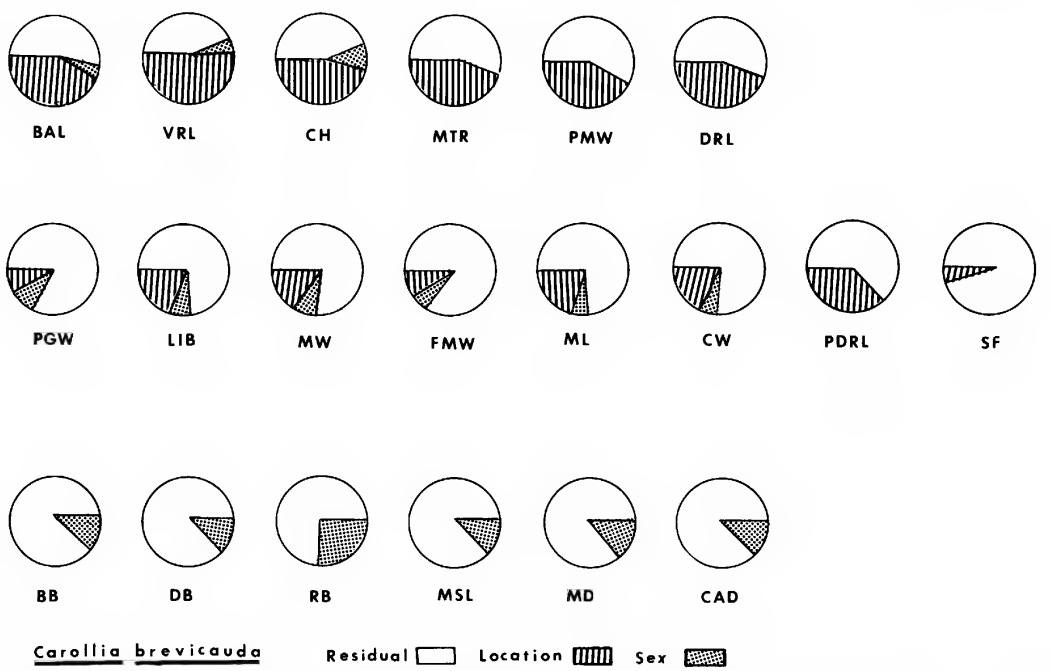

FIG. 6. Pie diagram of each character with percentage contribution to total variance for residual, sex, and locality for *Carollia brevicauda*. See figure 4 for explanation of character abbreviations.

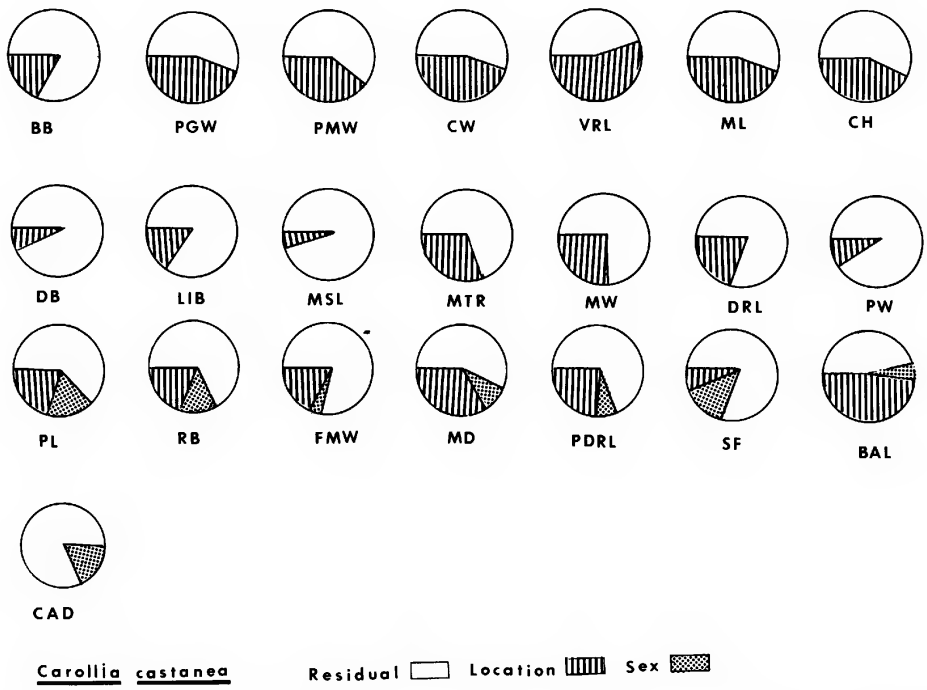

FIG. 7. Pie diagram of each character with percentage contribution to total variance for residual, sex and locality for *Carollia castanea*. See figure 4 for explanation of character abbreviations.

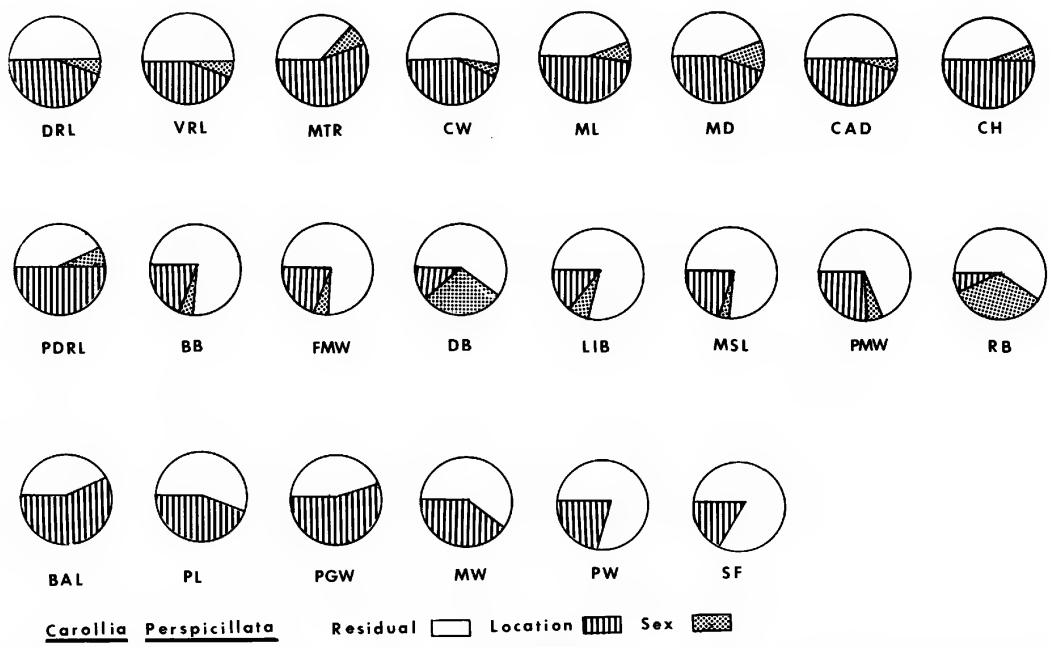

FIG. 8. Pie diagrams of each character with percentage contribution to total variance for residual, sex and locality for *Carollia perspicillata*. See figure 4 for explanation of character abbreviations.

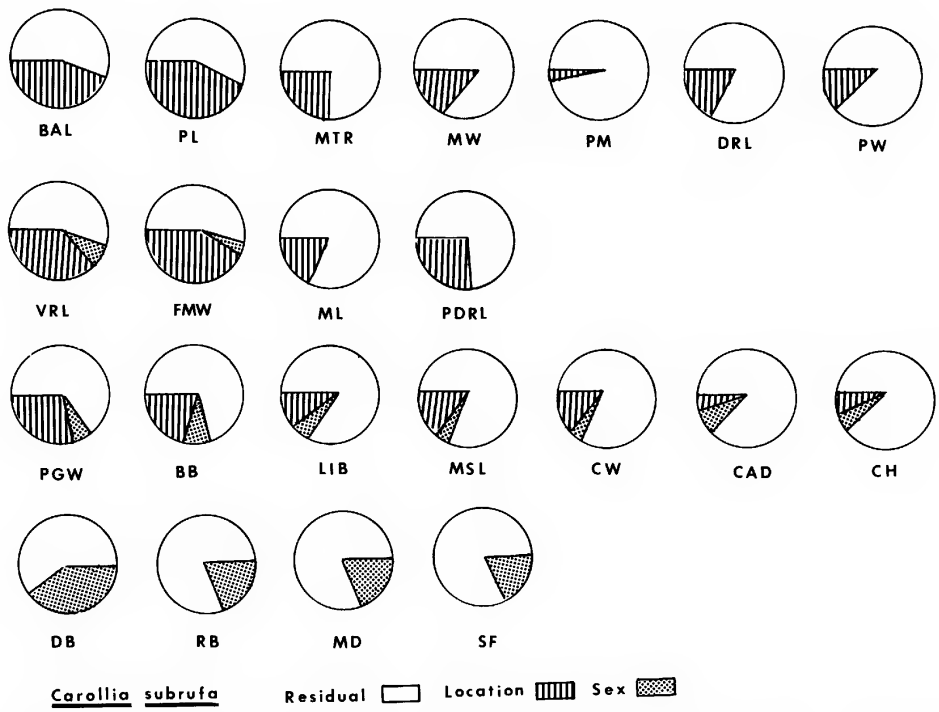

FIG. 9. Pie diagram of each character with percentage contribution to total variance for residual, sex and locality for *Carollia subrufa*. See figure 4 for explanation of character abbreviations.

SEXUAL DIMORPHISM

Sexual dimorphism is a relatively minor source of variation in all species of *Carollia* ranging from 4.07 percent of the total variation within species for *C. castanea* to 6.8 percent for *C. perspicillata*. Pine (1972) saw no average difference between the sexes except possibly in *C. perspicillata* where males were larger than females in average values for some measurements. This is considered in more detail in order to describe which characters differ between sexes. All species are considered because variance component analysis indicates that there are some morphological differences between sexes in each species and these have not been previously described.

Variance component analysis across characters for each species reveals differences in the distribution of dimorphism among the 22 characters. Specimens of *C. castanea* show very little sexual dimorphism. Only eight characters have a portion of their total variation due to sex; palatar length (sex component = 17.19%), coronoid angular (23.19%) and mandibular depth (18.26%) are most dimorphic. In contrast, *C. perspicillata* has a larger amount of character variance attributable to sex distributed throughout 16 characters; rostral breadth (36.65%), depth of braincase (19.4%) and mandibular depth (18.48%) show the greatest sex effects. *Carollia brevicauda* has 17 characters that vary between sexes; rostral breadth (24.31%), coronoid angular distance (20.89%) and mandibular depth (21.26%) have a relatively large sex component. *Carollia subrufa* has only 13 characters that vary between sexes, but several with a large proportion of the total variability attributable to sex: depth of braincase (35.65%), rostral breadth (21.88%), mandibular depth (29.93%) and slope of forehead (21.68%). All four species show dimorphism in mandibular depth and all but *C. castanea* have a relatively large effect on rostral width attributable to sexual dimorphism.

TABLE 4

Percentage of Total Variation Attributable to Locality, Sex and Residual from Four Populations of *Carollia castanea*[a]

Character	Locality	Sex	Within	Total
Basilar length	49.43	8.76	41.81	19.30
Palatar length	19.35	17.19	19.35	11.80
Postglenoid width	45.75	0.09	54.26	4.28
Breadth of braincase	18.18	0.0	81.82	3.23
Depth of braincase	6.79	0.0	93.39	3.48
Least interorbital breadth	19.06	0.0	80.95	2.60
Rostral breadth	18.79	9.68	71.34	2.24
Maxillary spur length	2.72	0.0	97.22	4.71
Maxillary toothrow	26.81	0.0	73.24	2.99
Width between first molars	23.76	0.0	76.75	2.28
Width between second premolars	38.33	0.0	61.64	4.80
Width between canines	43.22	0.0	56.77	2.02
Dorsal rostral length	19.43	0.0	80.53	6.23
Ventral rostral length	64.21	0.0	35.79	6.76
Palatal width	9.76	0.0	90.24	1.17
Foramen magnum width	17.57	1.41	80.98	3.05
Mandibular length	41.11	0.0	58.89	11.02
Mandibular depth	27.20	18.26	54.55	1.98
Coronoid angular distance	0.0	23.19	76.80	3.38
Coronoid height	35.78	0.0	62.43	5.75
Postdentary ramus length	21.14	4.25	74.68	3.95
Slope of forehead	3.75	5.93	90.37	9.60

[a] Total variation is the character variance over individuals, sex and locality.

Discriminant analysis between males and females, within species, over localities reveals a greater distinction between the sexes than noticed by Pine (1972). The species with the highest percentage of individuals correctly assigned to male or female (using cranial characters) was *C. subrufa,* with 94.37 percent correctly placed to sex. *Carollia brevicauda* had 88.14 percent and *C. castanea* had 80.33 percent correctly classified to male or female. Lowest is *C. perspicillata* with 79.4 percent placed to male or female correctly. Although *C. perspicillata* has a relatively large proportion of variability attributed to sex differences, discrimination is difficult due to the distribution of this variation among many characters that also vary with locality. *Carollia subrufa* has a much more restricted range with few characters that vary between sexes, but four have large variance components due to sex. This may in part explain the better discrimination between male and female *C. subrufa.*

The standard coefficients for canonical variates separating male and female *C. castanea* indicate that differences between sexes relate largely to larger basilar and mandibular lengths in males. Coefficients for *C. subrufa* identify depth of braincase as the primary variate for separating sexes. Males have a significantly deeper braincase than females. *Carollia brevicauda* has several characters with high loadings including: rostral breadth, dorsal and ventral rostral lengths. Only rostral breadth differs significantly between sexes. Males have wider rostrum than females. Ros-

tral breadth is also the most important character in distinguishing between male and female *C. perspicillata.*

The particular characters that appear to differ most between sexes of *Carollia* vary depending on the approach. The variance component analysis is indicating which characters vary in accordance to sex, given as a proportion of the total variance. Characters with a small variance, that only vary according to sex, will have a large sex component even though the differences between males and females may not be great. The canonical variates analysis identifies characters which can be used in discrimination. These characters have a greater magnitude of difference between sexes, even though the proportion of variation due to sex may not appear as large.

LOCALITY TRENDS

The four samples of *C. castanea* examined show a complex pattern of character variation using variance component analysis. All characters but one (coronoid angular distance) have some portion of their variability associated with location (table 4). An average of 29.25 percent of all variability within the 22 characters is attributed to differences in collecting locality. The characters with the largest locality differences (over 40% of the total) are postglenoid width, width between canines, ventral rostral length, basilar and mandible lengths.

Character trends in *C. castanea* were found to correspond with latitude. The southernmost population from Peru has the smallest values in all but two characters (dorsal rostral length and foramen magnum width). Scheffe's multiple range test identifies five characters that show significant differences between the Peruvian population and the other more northern populations. These characters are basilar length, palatar length, coronoid height, postdentary ramus length, and slope of forehead. The foramen magnum width is largest in the Peruvian sample composed of the smallest individuals. The pattern of geographic variation in basilar length illustrated in figure 10 is representative of variation in the other 15 characters, showing significant differences across populations with the exception of the foramen magnum width.

The distinctiveness of populations was examined using canonical variates analysis. The degree of differentiation is high among *C. castanea* samples (fig. 11). Classification results (from SPSS-DISCRIMINANT) placed specimens into their respective collecting localities with 98.4 percent accuracy, the high-

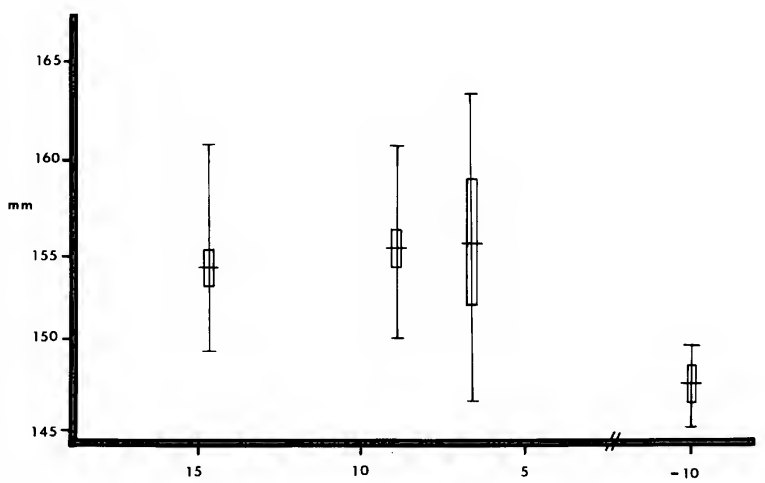

FIG. 10. Dice-Leras diagrams representing character trends for basilar length across latitudes (corresponding to collecting localities) for *Carollia castanea.* Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.

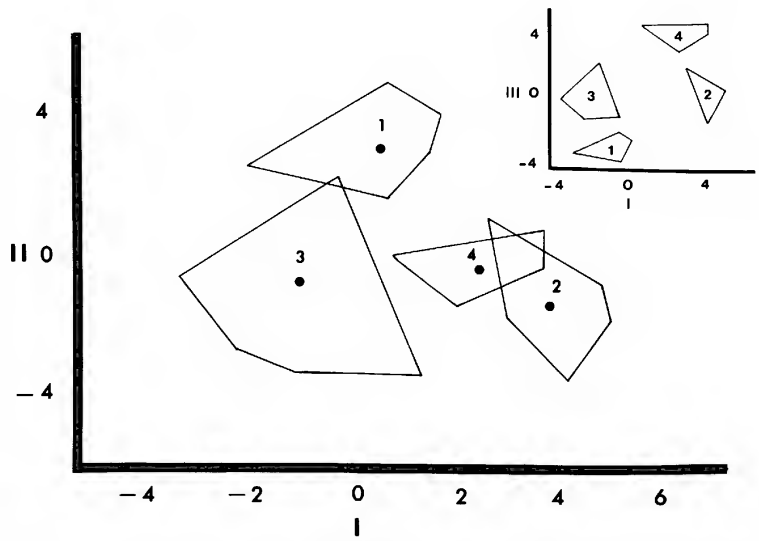

FIG. 11. Canonical variates analysis of four populations of *Carollia castanea.* Populations examined: 1. Rio Coco, Honduras; 2. Palamar, Costa Rica; 3. Tucarcuna Village Camp, Panama; Huanuco, Peru. All three canonical axes are represented one and two on the x and y axis, respectively. The third axis is diagrammed in the insert. Group centroids are represented by solid dots.

est of any of the samples of *Carollia* examined. The first canonical axis separates the samples from Costa Rica and Peru from the Panama sample. The population samples from Costa Rica and Peru appear more similar to one another than they are to that from Panama, which is curious. Standardized canonical coefficients for the first canonical axis indicate that variation in the width between the second premolars and breadth of braincase are most important in this separation. On the second canonical axis the sample from Honduras is separated from the other population sampled due to differences in the rostral breadth and width between canines. The third axis separates samples from Peru and Costa Rica; postglenoid width and coronoid height are important in this separation.

The eight population samples of *C. subrufa* examined had 16.02 percent of their total variation due to locality differences. Variance component analysis indicates that all but four characters vary with locality (table 5). Characters that vary most with location include basilar length, palatar length, ventral rostral length and foramen magnum width (all greater than 32% of total variation). Multiple range test results show only four characters that differ significantly among samples. The characters are: basilar length, palatar length, width between first molars, and foramen magnum width. The two southernmost populations sampled have significantly smaller values for these characters.

The two southernmost samples from Sabana Grande, Honduras, and San Antonio, Nicaragua have the smallest character means. Geographic trends in basilar length are illustrated in figure 12. This character represents variation in skull length across localities. The difference in size between the sampled northern and southern populations was also noticed by Pine (1972). These results show a stepped cline in character values.

Population samples of *C. subrufa* form two distinct subgroups using canonical variates analysis (fig. 13). This separation occurs along the first canonical axis with 40.19 percent of the variance explained. The six samples from Valle, Honduras and north into Mexico form one large overlapping group, whereas individuals from Sabana Grande, Honduras and San Antonio, Nicaragua are clearly distinct. In this separation, basilar length and slope of forehead are most important. The second canonical axis further separates populations ac-

TABLE 5

Percentage of Total Variation Attributable to Locality, Sex and Residual from Eight Populations of *Carollia subrufa*[a]

Character	Locality	Sex	Within	Total
Basilar length	47.69	0.0	52.31	18.17
Palatar length	42.38	0.0	57.62	9.19
Postglenoid width	28.65	1.31	70.02	3.17
Breadth of braincase	16.63	9.63	73.75	2.91
Depth of braincase	0.0	35.65	64.43	4.90
Least interorbital breadth	8.69	2.37	88.93	2.27
Rostral breadth	0.0	21.88	79.11	1.74
Maxillary spur length	7.43	0.84	91.18	3.10
Maxillary toothrow	24.50	0.0	75.61	2.71
Width between first molars	14.73	0.0	85.37	1.35
Width between second premolars	1.62	0.0	98.58	2.10
Width between canines	14.85	1.51	83.49	1.66
Dorsal rostral length	19.23	0.29	80.48	4.85
Ventral rostral length	32.71	7.25	60.03	2.29
Palatal width	13.63	0.0	86.47	0.82
Foramen magnum width	33.19	0.0	65.54	2.04
Mandibular length	21.54	0.0	78.45	7.24
Mandibular depth	0.0	20.93	79.34	1.90
Coronoid angular distance	1.61	3.41	94.96	3.66
Coronoid height	1.76	5.95	92.33	2.15
Postdentary ramus length	22.42	0.0	77.59	3.03
Slope of forehead	0.0	21.68	78.32	7.12

[a] Total variation is the character variance over individuals, sex and locality.

counting for 20.52 percent of the total variance. On this axis populations from San Antonio, Nicaragua and Sabana Grande, Honduras are separated from each other and the populations from El Salvador, Guatemala, and Nicaragua are separated from the northernmost populations from Mexico. Characters with high loadings on this axis are breadth of braincase, width between canines, and width between second premolars. The third axis separates the population from Valle, Honduras from the other populations with maxillary toothrow contributing most to group distinction.

Classification results (from SPSS-DISCRIMINANT) among population samples placed 100 percent of the individuals from El Salvador, Nicaragua, and Honduras into their respective collecting localities. These population samples are well differentiated from one another. The populations sampled from Mexico and southern Guatemala are not as distinctive; only 79 percent of the individuals were placed into their actual collecting locality.

The nine populations of *C. brevicauda* sampled had an average of 20.18 percent of the total variation due to locality differences. Variance component analysis of each of the 22 characters reveals that 16 characters have a locality effect (table 6). Eight characters contribute a large percentage (>26%) to the total variance. These include the basilar length, palatar length, maxillary toothrow length, width between first premolars, dorsal rostral length, ventral rostral length, coronoid height

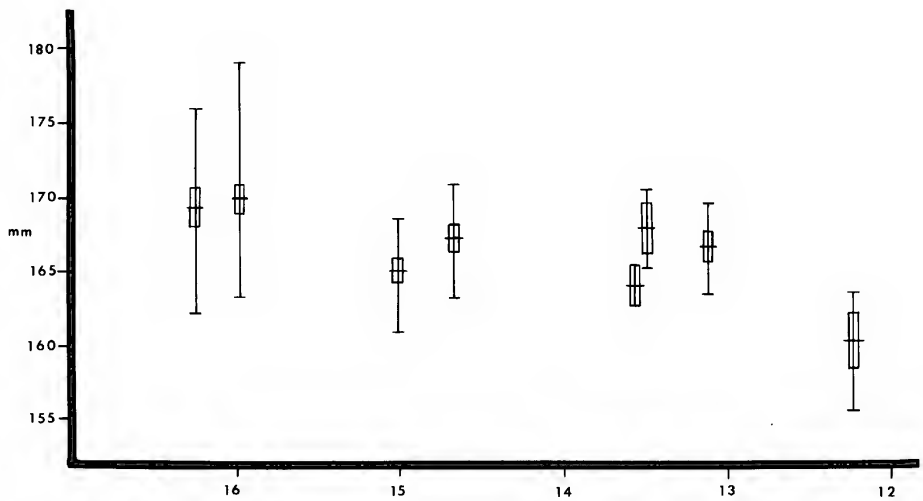

FIG. 12. Dice-Leras diagrams representing character trends in basilar length across latitude (corresponding to collecting localities) for *Carollia subrufa*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.

and postdentary ramus length. Multiple range test results show that 11 of the characters differ significantly between localities. Characters that are indicative of skull length (basilar, palatar, maxillary toothrow lengths, etc.) are significantly smaller in individuals from Ecuador than those from more northern populations. The sample from Panama has char-

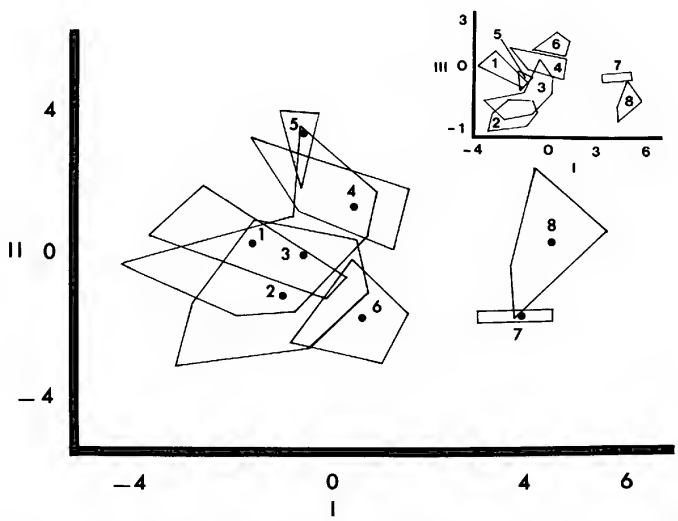

FIG. 13. Canonical variates analysis of eight populations of *Carollia subrufa* sampled. Populations included are: 1. Tapanetepec, Mexico; 2. Arriaga, Mexico; 3. Tapachula, Mexico; 4. Chiquimula, Guatemala; 5. La Libertad, El Salvador; 6. Valle, Honduras; 7. Sabana Grande, Honduras; 8. San Antonio, Nicaragua. The first and second canonical axes are represented by the x and y axes, respectively. The third axis is in the insert. Units on these axes represent canonical variates scores. Group centroids are indicated by solid dots.

TABLE 6

Percentage of the Total Variation Attributable to Locality, Sex and Residual from Nine Populations of *Carollia brevicauda*[a]

Character	Locality	Sex	Within	Total
Basilar length	44.51	2.90	52.79	30.67
Palatar length	42.72	0.0	57.28	18.45
Postglenoid width	11.76	8.29	79.96	6.50
Breadth of braincase	0.0	10.58	89.56	4.66
Depth of braincase	0.0	17.81	82.36	6.44
Least interorbital breadth	23.28	4.39	72.20	2.87
Rostral breadth	0.0	24.31	75.77	2.25
Maxillary spur length	0.0	12.30	87.70	3.68
Maxillary toothrow	38.11	0.0	61.88	5.95
Width between first molars	20.34	1.43	78.23	3.29
Width between second premolars	40.82	0.74	58.39	4.04
Width between canines	15.73	2.56	81.70	2.07
Dorsal rostral length	46.69	0.30	52.99	10.09
Ventral rostral length	37.09	1.27	61.73	5.50
Palatal width	17.18	0.0	82.20	1.56
Foramen magnum width	7.09	4.38	87.72	2.11
Mandibular length	23.54	7.78	68.68	19.03
Mandibular depth	0.53	21.26	78.24	2.10
Coronoid angular distance	0.0	20.89	79.11	5.70
Coronoid height	44.79	9.66	45.53	8.99
Postdentary ramus length	26.64	0.0	73.35	7.31
Slope of forehead	2.09	0.0	97.91	10.30

[a] Total variation is the character variance over individuals, sex and locality.

acter values that are significantly larger than those in the sample from Ecuador and the more northern populations.

Geographic trends in character values are illustrated for basilar, palatar, rostral, and maxillary toothrow lengths (figs. 14 and 15). These characters were chosen to represent the general patterns seen in the 22 measurements. There appears to be a clinal trend in palatar and dorsal rostral lengths, but a bimodal trend in the basilar and maxillary toothrow lengths from the same populations sampled. Palatar and dorsal rostral lengths are decreasing in length from north to south, whereas basilar and maxillary toothrow lengths are small in Nicaragua, increasing in Panama then becoming small again in Ecuador. The population from Panama has shorter palatar and dorsal rostral lengths and larger basilar and maxillary toothrow lengths, thus becoming more like *C. perspicillata.* Pine (1972) noted in his treatment of the species that *C. brevicauda* had a relatively long rear extension of the palate. This sample from Tacarcuna Village Camp, Panama appeared odd to Pine (1972). It has pelage characteristics resembling *C. subrufa*: short, sparse, coarse, indistinct, basal banding. He suggested the possibility of hybridization between *C. subrufa* and *C. brevicauda.* The greater length of the skull and shorter palate seen in the same specimens of *C. brevicauda* examined morphometrically suggests character convergence or possible hybridization with *C. perspicillata.*

Multiple range testing of characters identifies characters from the Tacarcuna Village Camp, Panama sample which are signifi-

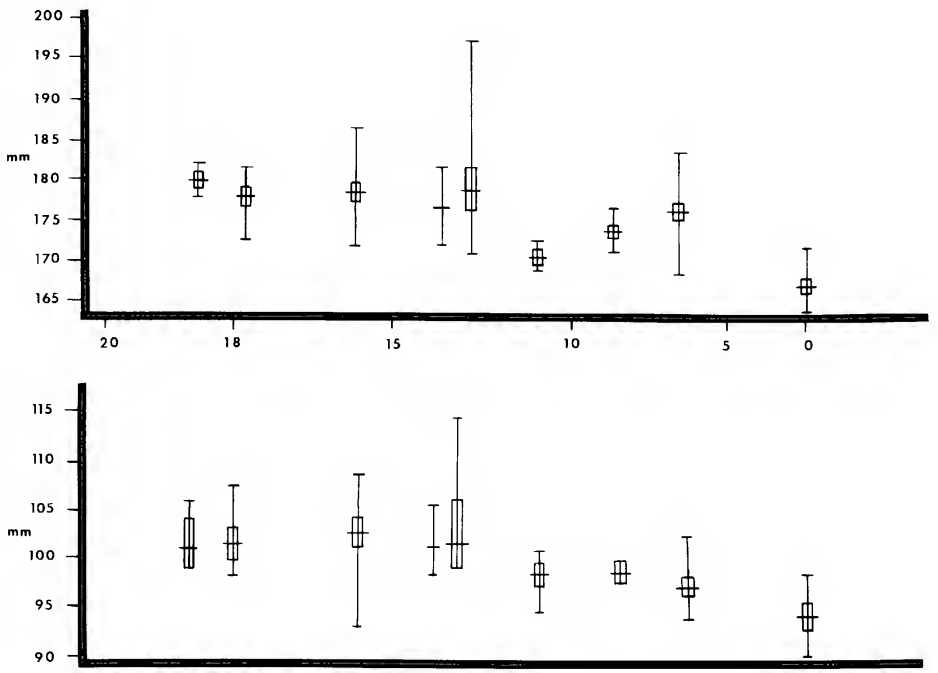

FIG. 14. Dice-Leras diagrams representing character trends in basilar (top) and palatar length (bottom) across latitudes (corresponding to collecting localities) for *Carollia brevicauda*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.

cantly larger than those samples from the northern populations; these are width between the second molars, palatal width, and maxillary length. These character differences indicate that there are shape differences, not only size differences, between this sample from Panama and the other population samples of *C. brevicauda*. The palatal width, not only its length, is greater.

Distinctiveness of the nine samples of *C. brevicauda* was examined using canonical variates analysis (fig. 16). A northern and southern grouping is formed along the first canonical axis, accounting for 47.87 percent of the total variation between population samples. The northern samples include individuals from Mexico south to Costa Rica. The southern two samples are from Panama and Ecuador. Characters with high loadings include width between the second premolars and basilar length. Individuals from Panama and Ecuador are separated from one another by the second canonical axis, which accounts for 20.95 percent of the total variance. Characters with high loadings are width between second premolars and width between canines. The third canonical axis further separates the northern individuals from Teapa, Mexico; Talanga, Honduras; and Cariblanco, Panama from the other populations sampled. This axis explains 14.81 percent of the total variation. Characters with high loadings include basilar length and width between canines.

Classification results place 79.66 percent of the *C. brevicauda* specimens in their correct collecting locality. Individuals from Ecuador are placed correctly 100 percent of the time, but only three specimens were examined. Those from Panama are next most distinctive with 92.7 percent correctly placed. The population samples from Guatemala and Honduras are not as distinctive. Individuals from Guatemala are difficult to place and only

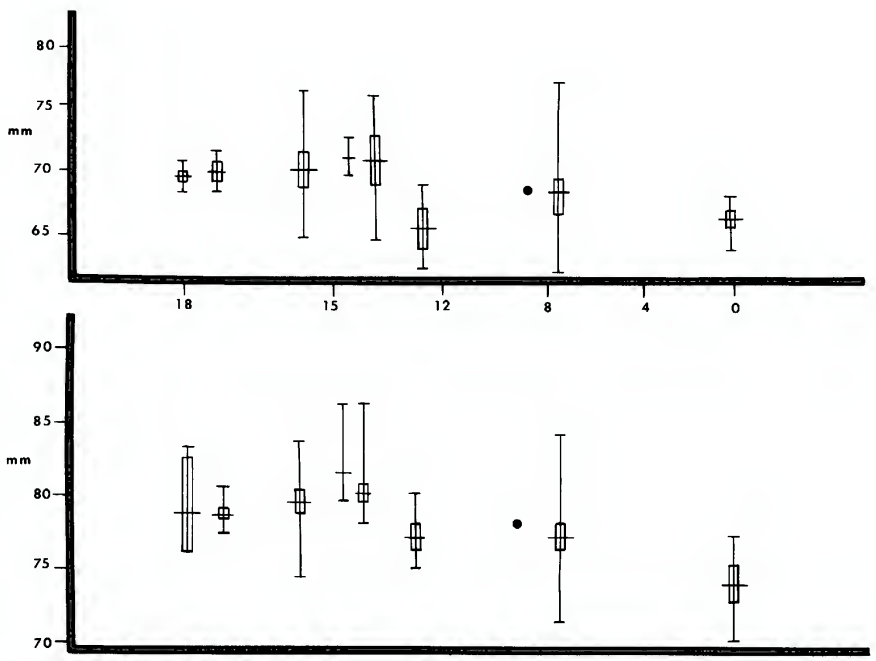

FIG. 15. Dice-Leras diagrams representing character trends in maxillary toothrow (top) and dorsal rostral length (bottom) across latitude (corresponding to collecting localities) for *Carollia brevicauda.* Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Dots represent population sample with equal character values. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for south latitude. The y axis indicates scale for character values.

58 percent fall into the actual collecting locality. The other 42 percent could just as easily be placed with the sample from Teapa, Mexico or Danli, Honduras. Those from Honduras are placed correctly 53 percent of the time. The other 47 percent are assigned to groups from the more northern localities.

The fifteen populations of *C. perspicillata* sampled had 34.6 percent of their total variation attributable to locality differences. Variance component analysis discloses locality effects in all 22 characters examined (table 7). Four of the characters have more than 50 percent of their variation due to locality effects; these include basilar length, postglenoid width, maxillary toothrow, and postdentary ramus length. Multiple range testing identifies 16 characters that differ significantly between localities. Characters that do not differ significantly between localities include least interorbital width, maxillary spur length, width between second premolars, palatar width, foramen magnum width, and slope of forehead.

Geographic trends in skull length for *C. perspicillata* are illustrated by correlating basilar length with latitude (fig. 17). The character trends are bimodal with large measurements from individuals from Mexico and Honduras as well as those from Bolivia, ruling out a smooth cline in character values corresponding with latitude. The samples from Paraguay and Brazil do, however, have character values significantly smaller than most of the more northern specimens examined.

A complex pattern of relationships is produced when canonical variates analysis is performed on all 15 samples of *C. perspicillata.* There is a great deal of overlap in the character values of individuals from different locations making interpretation difficult. Subsets of this one analysis are examined so that the relationships between individual

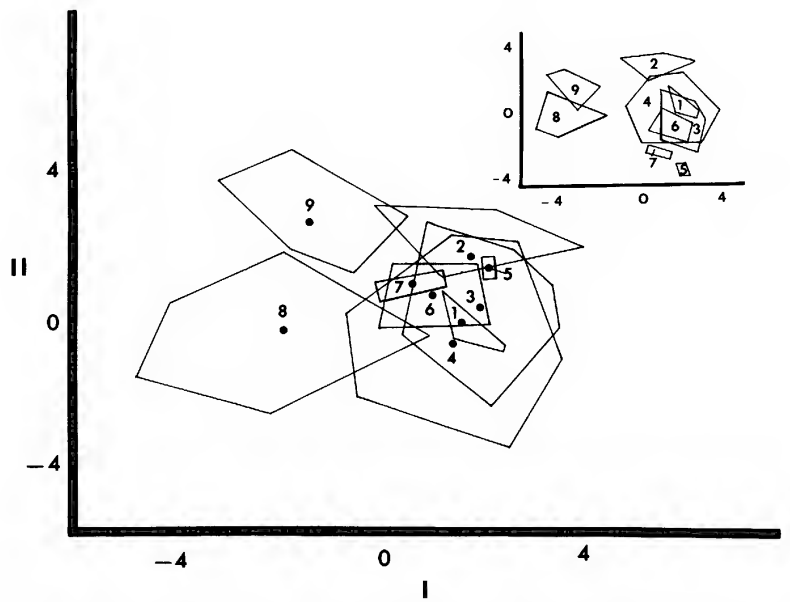

FIG. 16. Canonical variates analysis of nine populations of *Carollia brevicauda* sampled. Populations include: 1. Rio Quezalapam, Mexico; 2. Teapa, Mexico; 3. Puerto Barrios, Guatemala; 4. Danli, Honduras; 5. Talanara, Honduras; 6. Yalaguina, Nicaragua; 7. Alajuela Cariblanco, Costa Rica; 8. Tacarcuna Village Camp, Panama; 9. Puyo, Ecuador. The x and y axes represent the first and second canonical axes. The third axis is in the insert. Units on these axes represent canonical variates scores. Group centroids are represented by solid dots.

samples can be examined. First, samples with more than 12 individuals are examined separately (fig. 18). Individuals sampled from Mexico and Honduras are fully separated from the South American populations (which extend south and east of Colombia) on the first canonical axis. This first axis accounts for 49.09 percent of the total variance, with

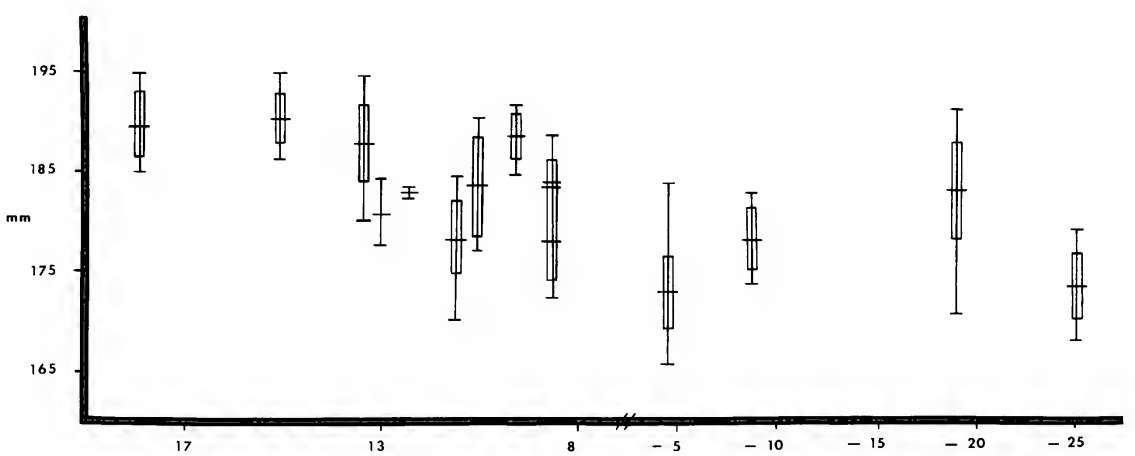

FIG. 17. Dice-Leras diagrams representing character trends in basilar length across latitude (corresponding to collecting localities) for *Carollia perspicillata*. Vertical lines show observed ranges; rectangles mark standard deviation; horizontal lines represent the mean for the population sample. Latitude is given along the x axis in degrees, a positive value is given for north latitude and a negative for the south latitude. The y axis indicates scale for character values.

TABLE 7

Percentage of the Total Variation Attributable to Locality, Sex and Residual from 15 Populations of *Carollia perspicillata*[a]

Character	Locality	Sex	Within	Total
Basilar length	66.79	0.99	32.22	50.75
Palatar length	46.41	0.0	53.59	24.63
Postglenoid width	55.77	0.0	44.23	11.99
Breadth of braincase	20.35	9.22	70.42	7.75
Depth of braincase	13.92	19.40	66.68	12.00
Least interorbital breadth	11.76	4.38	83.86	3.97
Rostral breadth	3.56	36.65	64.45	5.79
Maxillary spur length	23.87	7.17	75.19	6.27
Maxillary toothrow	53.66	4.29	42.05	10.04
Width between first molars	36.43	0.0	63.60	5.96
Width between second premolars	22.07	5.24	72.69	7.69
Width between canines	34.88	12.12	52.99	4.47
Dorsal rostral length	46.62	2.70	50.67	12.32
Ventral rostral length	46.12	1.31	52.52	8.24
Palatal width	22.86	0.0	77.14	1.94
Foramen magnum width	21.64	4.44	73.87	4.16
Mandibular length	48.44	7.39	44.15	32.79
Mandibular depth	38.43	18.48	43.04	6.32
Coronoid angular distance	39.79	7.58	52.63	14.95
Coronoid height	49.95	7.12	43.01	14.40
Postdentary ramus length	50.33	1.83	47.83	13.87
Slope of forehead	18.23	0.0	81.72	11.12

[a] The total variation is the character variance over individuals, sex and locality.

only basilar length loading highly. The most divergent population examined, from Tacaruna Village Camp, Panama, is separated from the other populations on the second canonical axis. Characters with high loadings on the second axis are basilar length, mandibular depth and coronoid-angular distance. The samples from Costa Rica and Panama are completely separated on this axis, which accounts for 11.9 percent of the total character variance. Along the third axis, individuals from Costa Rica, Colombia, and Peru are separated from each other. Characters with high loadings include maxillary toothrow length and coronoid-angular distance; 10.04 percent of the character variance is accounted for on this axis. Two more axes, the fourth and fifth, remain significant in this analysis and further separate individuals from Trinidad from the other populations sampled. Mandibular and palatar length have high loadings on the fourth and fifth axes, respectively.

Mexican and Central American samples of *C. perspicillata* are illustrated separately from South American samples, drawn from the canonical variates analysis which includes all populations (fig. 19). The Mexican and Central American population samples are separated very little on the first two canonical axes. The third axis, however, separates all the populations sampled. The individuals most differentiated here are those from two localities in Costa Rica (Palmar and Cariblanco) and one from 18 miles west-southwest of Chepo, Panama. The South American populations sampled (fig. 20) group tightly on the first three canonical axes. On the fourth

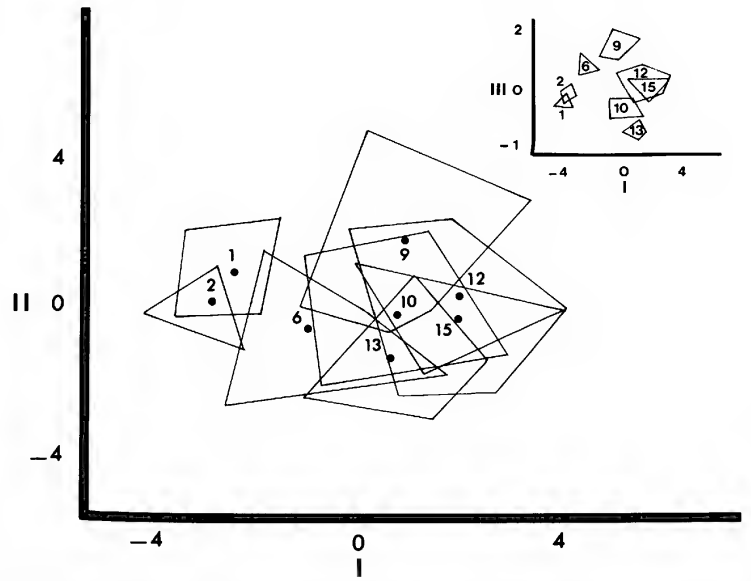

FIG. 18. Canonical variates analysis of eight populations of *Carollia perspicillata* sampled. All 15 populations were included in the analysis; only those with greater than 12 individuals are illustrated in this figure. Populations included are: 1. Teapa, Mexico; Rio Coco, Honduras; 6. Palmar, Costa Rica; 9. Madden Dam Road, Panama; 10. Valledupas, Colombia; 12. Rosarinho, Brazil; 13. Pucallpa, Peru; 15. Sapucay, Paraguay. The first and second canonical axes are represented by the x and y axes, respectively. The third axis separation is presented in the insert. Units along the axes represent the canonical variates scores. The group centroids for each population are represented by solid dots.

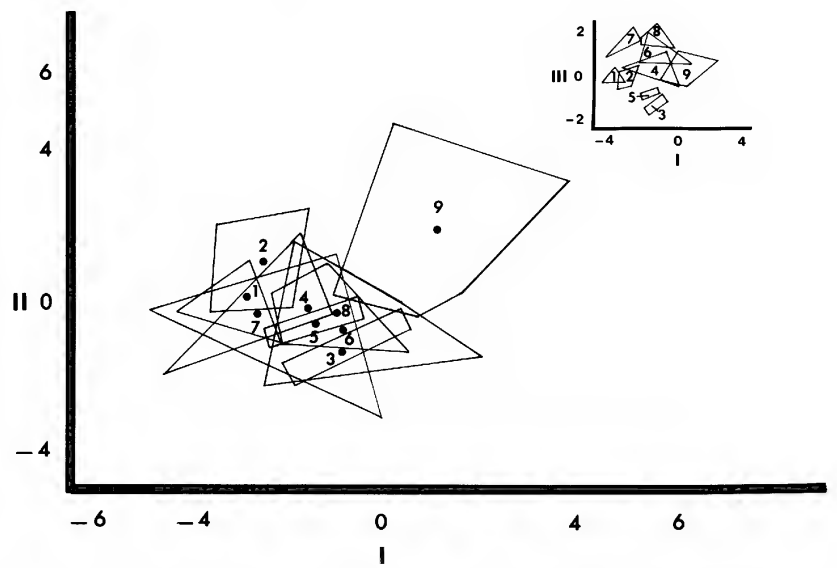

FIG. 19. Canonical variates analysis of *Carollia perspicillata* populations sampled, illustrating only Mexican and Central American populations. These include nine populations: 1. Teapa, Mexico; 2. Rio Coco, Honduras; 3. Sabana Grande, Honduras; 4. La Gatiada, Nicaragua; 5. Yalaguina, Nicaragua; 6. Palmar, Costa Rica; 7. Alejuela Cariblanco, Costa Rica; 8. R. de Panama; 9. Madden Dam Road, Panama. First and second canonical axes are represented by the x and y axes, respectively. The third axis is presented in the insert. Units along axes represent canonical variates scores. Group centroids are indicated by solid dots.

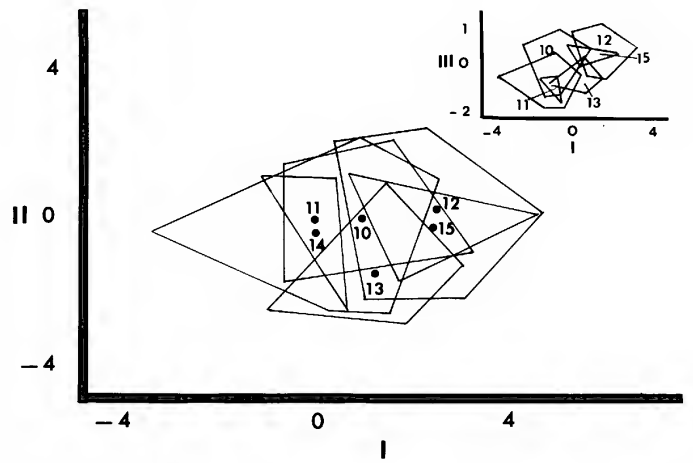

FIG. 20. Canonical variates analysis of *Carollia perspicillata* populations sampled, illustrating only those from South America. Populations include: 10. Valledupar, Colombia; 11. San Rafael, Trinidad; 12. Rosarinho, Brazil; 13. Pucallpa, Peru; 14. Buena Vista, Bolivia; 15. Sapucay, Paraguay. The first and second canonical axes are represented by the x and y axes, respectively. The third axis is indicated in the insert. Units along the axes represent the canonical scores. Group centroids are represented by solid dots.

and fifth, individuals from Trinidad are differentiated from specimens taken from the mainland. There is very little morphological differentiation among South American populations of *C. perspicillata.*

PHENETIC RELATIONSHIPS AMONG POPULATIONS

Cluster analysis was performed on population samples of all four species to examine how populations from throughout the range of each species group phenetically. Sample means of canonical variates for each of the 22 characters were used to calculate the squared Euclidean distance between populations. The average linkage method of Clustan's hierarchic fusion procedure was used for this analysis (Wishart, 1978). The average linkage method uses the average of all similarity coefficients for pairs of population samples, one from each cluster (Wishart, 1978). This procedure will find clusters of populations that are more similar within groups than between groups. This method for computing similarity coefficients attempts to take account of group structure. The clusters of populations produced are organized into a hierarchy based on similarity, which is represented in a phenogram.

The resulting phenogram (fig. 21) provides a summary of the phenetic relationships among the species populations sampled. The four samples of *C. castanea* cluster alone, in agreement with earlier taxonomic observations. The sample of *C. castanea* from Costa Rica is more morphologically differentiated from the other *C. castanea* populations sampled than are the other species from each other. The populations of *C. subrufa* sampled are divided into a northern group of six populations ranging from Mexico to Valle, Honduras and a southern group of two populations from Sabana Grande, Honduras, and San Antonio, Nicaragua. Between these two groups lie two samples of *C. brevicauda,* one from Teapa, Mexico and the other from Talanga, Honduras. The samples of *C. brevicauda* and *C. perspicillata* are ambiguous. As Pine had noticed, southern *C. perspicillata* and northern *C. brevicauda* show character convergence. Southern *C. perspicillata* appears as a subgroup within *C. brevicauda.* The northern population samples of *C. perspicillata* (ranging from Mexico to Panama) form a distinct group, except for three samples from within this range (Sabana Grande, Honduras; Palmar, Costa Rica; Canal Zone, Panama), which group with the South American populations sampled.

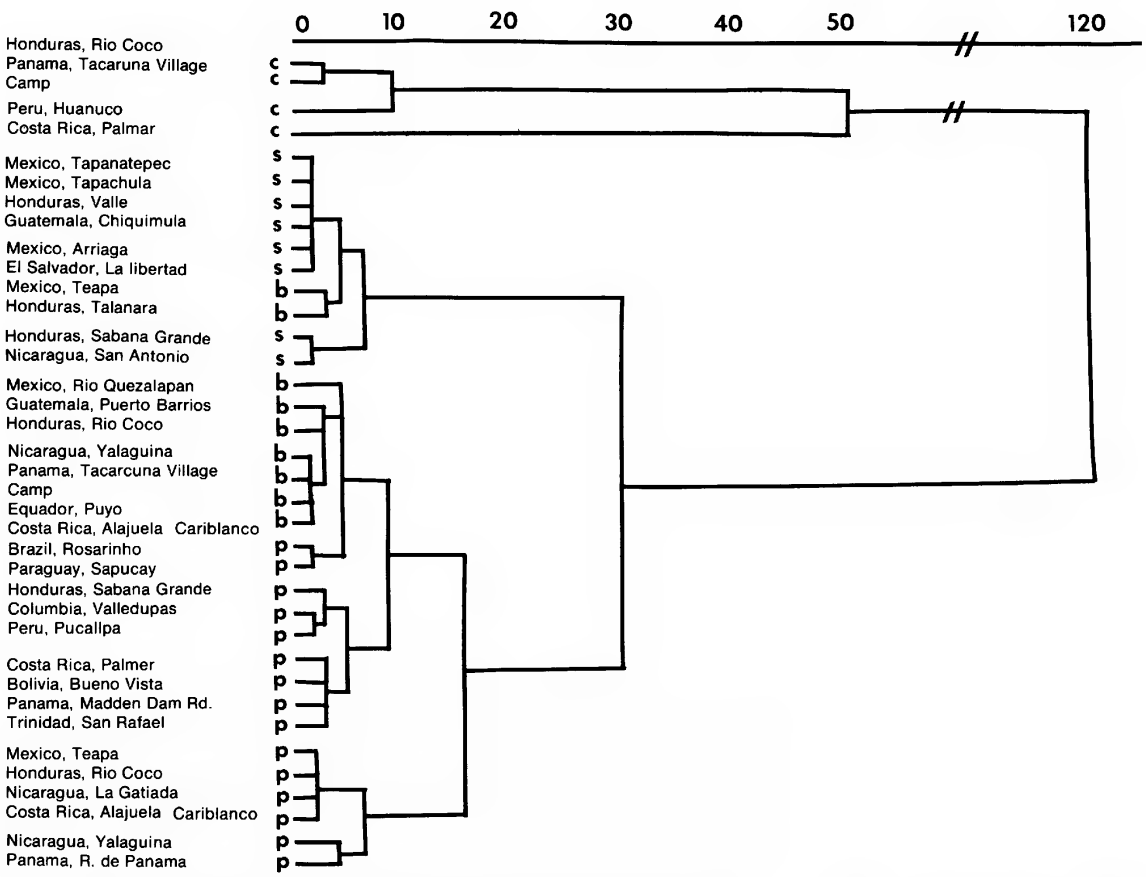

FIG. 21. Phenogram of all 36 samples of populations of *Carollia* resulting from cluster analysis. *Species abbreviations:* c—*castanea,* s—*subrufa,* b—*brevicauda,* p—*perspicillata.* Distance indicated across top of diagram.

Results of cluster analysis indicate that there are no clear morphological differences in the cranial characters examined between Central American and South American samples of *C. perspicillata* that correspond to the subspecific designation suggested by Pine (1972). According to him, specimens from north and west of the Amazon Basin have been assigned to *C. p. azteca* and those from the Amazon Basin and Parana drainage have been called *C. p. perspicillata* and *C. p. tricolor,* respectively. Cluster analysis does not consistently separate Mexican and Central American populations sampled, from South American samples, in correspondence with the North American *C. p. azteca* and the South American *C. p. perspicillata.* There is no clear distinction made among South American populations corresponding to the subspecies *C. p. perspicillata* and *C. p. tricolor.*

DISCUSSION AND CONCLUSIONS

In past taxonomic treatments of *Carollia* there has been little difficulty in distinguishing *C. castanea,* whereas *C. subrufa, C. brevicauda,* and *C. perspicillata* were not clearly defined until Pine (1972) recognized *C. brevicauda* in 1972. The phenetic relationship among the four species defined by Pine (1972), is clearly observed using canonical variates analysis. Results of canonical variates analysis agree with past taxonomic observations in identifying *C. castanea* as the most morphologically distinct species; *C. subrufa, C. brevicauda,* and *C. perspicillata* are less clearly

defined. *Carollia brevicauda* appears intermediate to *C. subrufa* and *C. perspicillata* in character values and shares phenetic similarity with both species. The intermediate nature of *C. brevicauda,* in part, explains the past difficulty in recognizing it as a distinct species. *Carollia subrufa, C. brevicauda,* and *C. perspicillata* are still difficult to distinguish when relying on classical means. Overlap in character values between populations of *C. subrufa* and *C. brevicauda* and also between *C. brevicauda* and *C. perspicillata* populations may be the reason for this continuing difficulty in species distinction.

The specimens left unidentified by Pine (1972) were easily assigned to existing species using discriminant function analysis. Unknowns were placed with the species having the closest group centroid and thus the greatest similarity in cranial measures examined. This does not mean that these specimens are necessarily members of the species that they are placed with, but that this is the most likely group membership. The specimen from Kartabo, Guyana (=British Guiana) was placed with *C. subrufa* in my analysis. This specimen may represent a range extension for *C. subrufa* as there has been none recorded south of Nicaragua. Pine notes external features such as pelage which resembles that of *C. brevicauda* and that size is small as that in *C. castanea.* The teeth, however, do resemble those of *C. subrufa.* It is easy to see here that when all factors are considered, identification to species is complicated, since not all features agree. Examination of more specimens from Guyana would be useful to determine if there is a disjunct population of *C. subrufa* in Guyana not previously noted. The specimen from Napo Pastaza, Ecuador was placed with *C. brevicauda* using skull characters. Pine also wanted to place this specimen with *C. brevicauda,* but its small size excluded it from other *C. brevicauda* taken at the same locality. The specimen from San Juan, Peru was placed with *C. perspicillata.* Pine noted that this specimen's skull was reminiscent of both *C. perspicillata* and *C. brevicauda,* and that it was larger than any *Carollia* from that far south, its central lower incisors are small for *C. perspicillata* and its body hair is long and tricolored as found in *C. brevicauda.* The two specimens mentioned above were considered as possible undescribed species by Pine (1972). The last unidentified specimen was an old female with worn teeth and pelage, which Pine identified as *Carollia* but could not place to species. He thought it was either *C. subrufa* or *C. brevicauda*; discriminant analysis placed it with *C. brevicauda.*

The most important source of variation in the values from cranial measurements within species of *Carollia* is the individual variance component, which averaged over species, accounts for 69 percent of the total variation. The potential causes for this variability include measurement error, response to changing environment, sampling more than one biological population, and random change and unexamined environmental effects. A portion of this residual variation can be explained by measurement error which is on the average only 5 percent of the total variation. Other factors must also be contributing to this large amount of individual variation.

The variables exhibiting high residual variance components (LIW, MSL, MW, FMW, MD, SF) were not examined in Pine's (1972) treatment of the genus. These characters are of no use in distinguishing among species because they are more variable within species than among. Taxonomists often look for characters that can be used consistently to distinguish between species without discussing the significance of those characters which vary in accordance with other factors.

Differences in cranial and mandibular measurements in species of *Carollia* can be viewed from a functional standpoint. Characters examined in this study such as coronoid height, coronoid-angular distance, and mandibular depth have been related to possible functional differences in molossid bats by Freeman (1981). She suggests that a thickening of the dentary and an increase in the area for insertion of the temporalis muscle at the coronoid process may be related to a diet consisting of hard-shelled foods. Both coronoid height and coronoid-angular distance measurements differ significantly among species of *Carollia*; values are the greatest for *C. perspicillata* followed by *C. brevicauda, C. subrufa* and then *C. castanea.* This sequence corresponds to the general size difference among species, indicating that *C. perspicillata* is capable of consuming larger and

TABLE 8
Characters with High Residual Variance Components for *Carollia* Species[a]

C. castanea		*C. subrufa*		*C. brevicauda*		*C. perspicillata*	
MSL	97.2	PMW	98.6	SF	98.0	LIB	83.9
SF	96.4	CAD	95.0	BB	89.6	SF	81.7
DB	93.4	CH	92.3	MSL	87.7	MSL	75.2
PW	90.2	MSL	91.3				

[a] Variance components expressed as a % of the total variance. For abbreviations see legend for figure 4.

tougher food items than the other species, possibly opening up resources unavailable to the others. This may in part explain the large geographic range of *C. perspicillata.*

Foraging patterns unique to individuals of the same species may be contributing to this high individual variation. Heithaus and Fleming (1978) studied the foraging pattern of *C. perspicillata* in Costa Rica during the wet seasons and found that individuals used the same feeding areas consistently with very little overlap among individuals. Feeding on fruits which differ in thickness of skin and texture could cause a change in the magnitude of forces acting on the skull and mandible produced by the muscles of mastication: the masseter and temporalis. Bone thickens at points where more stress occurs (Hildebrand, 1974; Buckland-Wright, 1978). The bones in the mammalian skull undergo a constant remodeling by absorption and deposition of bone tissue that may be functionally influenced (Straney, 1983). These areas of active remodeling represent the most plastic regions of the skull. If the individuals within a population have consistent differences in the food eaten, the areas where the muscles involved in mastication originate and insert would be the most variable. Comparison of the areas of origination and insertion to regions of the skull and mandible with high residual variance components shows a fair correspondence (table 8).

Maxillary spur length has a high residual variance component across *Carollia* species. The maxillary spur is the anterior portion of the incomplete zygomatic arch where the masseter originates. The posterior mandibular regions include the coronoid-angular distance and coronoid height and have a large residual component in *C. subrufa.* These regions are insertion sites for the masseter and the temporalis. It is possible that the effects of resource partitioning among individuals of the same species population may be contributing to this high individual variance in character values.

There are, however, other explanations for the high variability in a few of these characters. The maxillary spur is a cranial feature which is prone to damage because of its shape (long and narrow) and position (extending laterally). The slope of forehead was one of the more involved measurements to take and thus may have a larger error due to measurement technique. There are aspects of the population structure not yet considered as potential cause for this larger residual component of variation seen within populations.

A biological population can be defined as a group of interbreeding individuals that breed more among themselves than with other such populations. In bats, a biological population may consist of only the individuals occupying one roost site. When specimens are collected with a mist net, there is no assurance that only the individuals from one such population are taken. It is possible that individuals from several biological populations are represented in each population sample. Individuals from different biological populations are likely to differ due to genetic divergence. This genetic divergence may be reflected in morphological variation within populations. This is one more level at which *Carollia* may be organized and at which variation is occurring. The data in this analysis are purely morphological, so genetic differentiation cannot be compared to morphological differences between populations.

Factors, such as random genetic variability, growth after epiphyseal fusion of the

metacarpals and unexplained environmental effects, must also be considered as potential sources of variation. Genetic variability is present among species of *Carollia* (Straney, 1980) but genetic variation among populations has not been examined in detail. The specimens examined were taken over a span of 100 years; environmental change has most likely occurred during this time. Changing environmental factors provide an external influence which may affect morphology.

Secondary sexual dimorphism contributes a small proportion to the total variation within each species, but is present to varying degrees within all species of *Carollia.* Males are larger than females in all species. This is commonly seen in other kinds of mammals. The adaptive significance most often assigned is Darwinian sexual selection, whereby males must compete for mates and because it is advantageous, large body size is selected (Darwin, 1859). This is one possible explanation, but little is known about the breeding behavior of *Carollia* except that Porter (1975) noticed harem behavior in a laboratory colony of *C. perspicillata.* Other phyllostomid bats in which males are larger than females are *Uroderma bilobatum* (Baker, Atchlley, and McDaniel, 1972), *Phyllostomus discolor* (Power and Tamsitt, 1973; Bradbury, 1977) and *Anoura cultrata* (Nagorsen and Tamsitt, 1981). The opposite is seen in *Ametrida centurio* (Peterson, 1965), females are so much larger than males that they were once considered to be separate species. This is also seen in some vespertilionid bats, particularly in wing dimensions (Myers, 1978). This trend has been associated with a need to compensate for extra loading of pregnancy and the transport of young, coined the "Big Mother" hypothesis by Ralls (1976). Female *Carollia* also must deal with the extra loading of pregnancy and carrying young. Examination of Pine's (1972) data indicates that females have forearm lengths equal to those of the males, who are larger in weight. The wing dimensions of females appear longer relative to body size, which may compensate for the extra loading of pregnancy.

Sexual dimorphism differs in degree and in the characters that vary among species of *Carollia. Carollia subrufa* and *C. brevicauda* are the most dimorphic. They share a number of characters that vary most between sexes, with no locality effects. These include depth of braincase, rostral breadth and mandibular depth, which are larger in males. From values of these measurements, it appears that males in these two species have a deeper braincase and a wider muzzle than do females. The other two species of *Carollia* are less sexually dimorphic in terms of my ability to discriminate between males and females in the samples. Rostral breadth is the most important character exhibiting sexual dimorphism in *C. perspicillata,* with little sexual dimorphism in a large number of characters. Many of the characters that vary little between sexes also have locality effects that may reduce the effectiveness of discrimination between males and females. Least dimorphic is *C. castanea.* Very few characters are involved and only palatar length and coronoid-angular distance have a large variance component due to sex. Pine (1972), using classical methods, had noticed an average difference between values from male and female cranial measurements only for *C. perspicillata.* He had not noticed differences between the sexes for the other species. The reason for these differences among species is impossible to interpret from my data, but may be explained by studying the differences in social structure and behavior of *Carollia* species.

Geographic differences in values from cranial measurements are seen in all four species of *Carollia.* Past taxonomic problems can in part be attributed to an attempt to combine specimens from throughout the range of each species without taking geographic variation into account. This variability between collecting localities was first described in general terms by Pine (1972) who noticed regular differences among populations of *C. subrufa, C. brevicauda,* and *C. perspicillata.* Morphometric examination of cranial features reveals a latitudinal trend in skull length in all species of *Carollia.* Individuals from the northern portion of the range of each species are consistently larger than those from the southern portion. Similar patterns have been found in other phyllostomid bats. Nagorsen and Tamsitt (1981), for example, revealed an increase in size from south to north for *Anoura cultrata.*

Latitudinal size trends are seen in many

different animal groups. Johnson and Selander (1972) found a large size factor associated with climate in North American house sparrows. Rees (1970) found that a size factor in measurements on white-tailed deer correlated positively with latitude. The biological significance of these size trends seen in a variety of animal species is not clear. The usual assumption is this increase in size along a latitudinal gradient must have some adaptive significance.

Bergman's rule has been used to explain an increase in body size from south to north, with animals in cooler (more northern) environments tending to have larger body size to provide a smaller relative surface area. The adaptive advantage gained is an increase in heat retention efficiency. One problem with this explanation in the case of *Carollia* is that size would be expected to increase as a function of distance from the equator, but individuals from south of the equator in Bolivia (25°S latitude) are smaller than those from closer to the equator. Another problem is that the northernmost and southernmost populations are still in a warm climate; Bergman's rule is usually associated with populations of the same species which are found in both a cold and a warm climate. It seems likely that other principles are operating.

Another hypothesis used to explain an increase in size in more northern populations, advanced by Grant (1965) and Heaney (1978), is based on the assumption that interspecific competition is greater in species-rich areas, like the tropics, and so selection favors smaller-sized individuals that can occupy more specialized feeding niches. By the same reasoning, areas with fewer species should have less competition for resources and so selection may favor larger size so that a wider range of resources can be utilized. The smallest *Carollia* do come from tropical South America and the largest are from Mexico, but detailed ecological data are lacking for each of the populations sampled. There are, however, fewer phyllostomid, glossophagine, and total bat species in Central America than in South America (Nagorsen and Tamsitt, 1981). With fewer species of bats in Central America, a greater variety of food may be available to *Carollia* species and so there may be a selected advantage for larger size. The general trend in bat species diversity does display differences across the range of *Carollia* species that are concordant with the size change within these species. McNab (1971) suggested that latitudinal change in body size may be the result of the distribution of food species, or of competitors for the same food resources. An interaction between these factors is likely.

The populations of *C. castanea* sampled are very distinct from one another. Pine had noticed differences in the average measurements among *C. castanea* population samples. The differences among the four localities sampled were greater than those between any of the other species populations; the sample from Costa Rica is particularly distinctive. A reduction in gene flow through geographic distance may account for differences in measurements among samples. *Carollia castanea* is known to be habitat specific preferring tropical evergreen forests and to have a relatively small home range (Handley, 1966; La Val, 1970). These factors may be enough to hinder gene flow, allowing small populations of *C. castanea* to differentiate more than other species. A closer look at *C. castanea* would be interesting to see if this apparent divergence is genuine, not just a function of the small number of populations sampled in this study.

Geographic differentiation is well developed in the *C. subrufa* sampled. *Carollia subrufa* has the smallest geographic range of any of the species of *Carollia.* It is distributed from Mexico to Honduras, occupying primarily the Pacific coast side of the Sierra Madre. *Carollia subrufa* is the only species of *Carollia* throughout most of its range. It occurs sympatrically with *C. perspicillata* in Chiapas and Nicaragua, and with *C. brevicauda* on the gulf coast side of Honduras. *Carollia subrufa* is primarily an inhabitant of tropical deciduous forests. Samples from Honduras and Nicaragua cluster separately from the more northern populations sampled. The southern populations are smaller in skull and mandibular lengths than the northern populations. One possible explanation for this divergence is character displacement, due to contact with other *Carollia* species in this southern portion of the range.

This has been described in birds and mammals by Grant (1972, 1975). Selection acts against similarity between sympatric populations of two systematically related species (as compared to their allopatric populations) so that they do not compete for food or mates. Pine (1972) makes note of collecting *C. brevicauda* in the same net as *C. subrufa* in Honduras, 2 mi west of San Pedro Sula. At this location he noted an exaggerated difference between the two species and suggests the possibility of character displacement. The *C. subrufa* sampled from Sabana Grande, Honduras, and San Antonio, Nicaragua, the regions where sympatry is likely, are very distinct from the more northern populations where *C. subrufa* occurs allopatrically from *C. brevicauda.* In order to be sure that character displacement is occurring, a large sample of *C. subrufa* and *C. brevicauda* caught at the same location is needed for comparison. Such specimens could be compared to known allopatric populations of the same species. Pine treats *C. subrufa* as monotypic, but notes that individuals from the northern part of their geographic range are larger than those of the southernmost part, and specimens taken west of the Isthmus of Tehuantepec have hairier forearms than do those from east of the Isthmus. He suggested that with examination of more specimens, the existence of subspecies may become apparent. Both canonical variates analysis and cluster analysis identify a distinct southern population of *C. subrufa* that may represent a recognizable subspecies.

Carollia brevicauda is widely distributed and complementary to *C. subrufa* along the wet Gulf-Caribbean coast of Central America, north of Honduras. It has been collected sympatrically with *C. castanea, C. subrufa,* and *C. perspicillata.* There may be character displacement occurring between *C. brevicauda* and *C. perspicillata.* Pine (1972) has mentioned that specimens of these species taken from the same collecting locality are more easily distinguished from those from allopatric populations. The populations of *C. brevicauda* from Teapa, Mexico and Talanga, Honduras cluster with *C. subrufa.* This divergence may represent character displacement between *C. brevicauda* and *C. perspicillata.* Sympatric populations of *C. brevicauda* and *C. perspicillata* were not examined from Teapa, Mexico or Talanga. Sympatric populations from Rio Coco, Honduras, Yalaguina, Nicaragua, and Alajuela Cariblanco, Costa Rica were examined and do show a large morphological distance in the cluster analysis results. Character displacement may be occurring between *C. brevicauda* and *C. perspicillata*, another potential source of intraspecific variation that must be considered at the population level.

Discriminant analysis of *C. brevicauda* separates the individuals from Panama and Ecuador from the more northern populations sampled. The divergent population sample from Panama corresponds to an unusual population noticed by Pine (1972), which he first regarded as a hybrid swarm of *C. subrufa* and *C. brevicauda.* Externally, they lack the hairiness of the forearm normally seen in *C. brevicauda.* The skull dimensions differ in palatar and dorsal rostral lengths, decreasing in length, whereas the maxillary toothrow and basilar lengths increase. These differences in dimension are evident when correlating character means with latitude. The decrease in palatar length and increase in maxillary toothrow length are changes toward a more *C. perspicillata*-like skull, which suggests possible character convergence or hybridization with *C. perspicillata,* not *C. subrufa* as suggested by Pine (1972).

Carollia perspicillata is the most widespread and common of the four species. It is found in both tropical evergreen and deciduous forests. Bloedel (1955) noted that individuals may be found solitary or clustered in colonies of as many as 1000 individuals. Greenhall (1959) wrote that it "is probably the most abundant fruit eating bat in the American tropics." Darwin (1859) observed that the wide-ranging and common species tend to be the most variable. When the percentage contributions to the total variance due to locality is compared among species of *Carollia,* variation increases with an increase in the size of the species range. The highest value of 34.6 percent is found in *C. perspicillata,* the most wide-ranging species. The lowest value of 16.0 percent is that of *C. subrufa,* with the most restricted geographic

range. Darwin's prediction is right in this case. This is not surprising, as *C. perspicillata,* the most wide-ranging and common species in the genus, must adapt to many local environments.

Geographic differentiation in cranial dimensions is greater among samples of *C. perspicillata* than among samples of any other species of *Carollia.* The northern samples from Mexico and Honduras can be distinguished from the southernmost samples from Peru, Bolivia, and Paraguay, but samples taken from regions in between have intermediate character values. There is no clear division between samples from north and west of the Amazon Basin and those from the Amazon Basin itself that corresponds to the subspecific designation *C. p. azteca* and *C. p. perspicillata,* respectively. Nor is there a clear division between the subspecies *C. p. perspicillata* and *C. p. tricolor* from the Amazon Basin and Parana drainage, respectively, when considering cranial morphology alone. Pine distinguished *C. p. azteca* from *C. p. perspicillata* on the basis of its larger size, and distinguished *C. p. tricolor* from *C. p. perspicillata* on the basis of its small size, soft tricolor pelage, and hairy forearms and toes. The characters used by Pine (1972) were all external features; mine were cranial measurements. This indicates that the pattern of variation in cranial morphology varies independently from the external features used by Pine (1972) to distinguish between samples of *C. perspicillata* from different geographic regions.

Two of the southernmost *C. perspicillata* populations sampled (Rosarinho, Brazil; Sapucay, Paraguay) cluster with northern samples of *C. brevicauda.* This agrees with Pine's (1972) observations that the southern *C. perspicillata* are morphologically similar to northern *C. brevicauda.* Southern *C. perspicillata* are small (relative to northern individuals) and northern *C. brevicauda* are large (relative to southern individuals), so a size factor may in part be responsible for this similarity. External features are also shared, including hairy forearms and toes, characteristic of *C. brevicauda.*

Affinities among the species of *Carollia* can be reexamined in light of my morphometric findings. Pine (1972) has suggested that Central America may be the center of origin for the species of *Carollia,* since they all co-occur there, and *C. subrufa* occurs nowhere else. The continental divide may have played a major role in forming a barrier to gene flow leading to the differentiation of *C. subrufa* and *C. brevicauda* from a common ancestor (Pine, 1972). Using classical techniques, Pine (1972) postulated that the relationship between species went: *C. perspicillata–C. brevicauda–C. subrufa–C. castanea*—representing a sequence from least modified to most highly modified from a common ancestor. My morphometric results provide a distance (Mahalanobis distance = the Euclidean distance squared in the 3 dimensional space defined by the canonical variates) between each pair of species. Mahalanobis distance between *C. castanea* and the other species is greater than the distance between any of the other species, indicating that *C. castanea* is the most phenetically divergent, as Pine (1972) also noted. The phenetically closest species are *C. subrufa* and *C. brevicauda,* and these are about equidistant from *C. perspicillata* in canonical variates analysis. Cluster analysis provides slightly different results: *C. brevicauda* and *C. perspicillata* cluster together equidistant from *C. subrufa.* Canonical variates analysis results are probably a better representation of phenetic affinity between species because separation occurs in multidimensional space rather than the two dimensions of cluster analysis. Both techniques indicate that *C. brevicauda, C. perspicillata,* and *C. subrufa* have similar values for cranial measurements.

Another source of data that can be considered is chromosomal morphology. There is an X-autosomal translocation in all *Carollia* populations examined, except for some of the *C. castanea* from Peru (Patton and Gardner, 1971). Heterochromatin patterns (in C bands) of *C. brevicauda* and *C. perspicillata* are very similar, but the chromosomes of *C. castanea* lacked much of the heterochromatin common to the other two species (Stock, 1975; *C. subrufa* was not examined by Stock). The lack of a chromosomal translocation in some of the Peruvian *C. castanea* indicates that either this population has lost the trait or all the others gained the translocation at some point during the evolution of *Carollia.* Het-

erochromatin patterns further indicate the uniqueness of Peruvian *C. castanea* and the similarity of *C. brevicauda* and *C. perspicillata.* This chromosomal affinity agrees with the morphological similarities and differences between these three species.

Isoelectric focusing results group *C. castanea* and *C. perspicillata* and also *C. brevicauda* and *C. perspicillata* (Straney, 1980). The distinctiveness of *C. castanea* is evident in the morphological and chromosomal data, but the electrophoretic data show possible convergence between *C. castanea* and *C. perspicillata.*

The most morphologically and chromosomally derived species is *C. castanea.* The relationships among *C. subrufa, C. brevicauda,* and *C. perspicillata* are more problematic due to conflicting information. An association between *C. brevicauda* and *C. perspicillata* is found most often; morphological, heterochromatin (C banding) and isoelectric focusing results agree. The position of *C. subrufa* is not clear. Values from cranial measurements place it closest to *C. brevicauda.* The geographic distribution of *C. subrufa* and *C. brevicauda* indicates they may have split from a common ancestor in southern Mexico and Central America and spread north on separate sides of the Sierra Madres where they speciated allopatrically. The possible convergence between *C. castanea* and *C. perspicillata,* identified by isoelectric focusing data, is not evident in cranial morphology or chromosomal data.

The relationships between species that can be constructed are numerous. The affinity between *C. castanea* and any of the other *Carollia* is unclear; morphologically it is closest to *C. subrufa,* whereas biochemically it is closest to *C. perspicillata.* The species *C. subrufa* and *C. brevicauda* are phenetically very similar and have a geographic distribution which suggests a split from a common ancestor. *Carollia perspicillata* and *C. brevicauda* show a close affinity at all levels considered. There is not one diagram that can be used to represent species affinity that fully agrees with all sources of information available. The direction of change is difficult to determine, as is the point of the original divergence of the species of *Carollia.*

The results of this study confirm much of the past observations concerning morphological variation within and among *Carollia* species. Patterns of variation are more apparent and can better be compared when morphometric techniques are applied to problematic groups such as *Carollia.* The morphometric techniques used allowed quantification of the relative amounts of variation due to species, locality, sex, and individual differences which could not be achieved by classical means. From this information, hypotheses concerning the underlying causes for these observed differences can be advanced and, when possible, tested.

LITERATURE CITED

Baker, R. J., W. R. Atchlley, and V. R. McDaniel
1972. Karyology and morphometrics of Peters' tent making bat *Uroderma bibobatum* Peters (Chiroptera: Phyllostomatidae). Syst. Zool., vol. 21, pp. 414–429.

Bloedel, P.
1955. Observations on the life histories of Panama bats. Jour. Mammal., vol. 36, pp. 232–235.

Bradbury, J. W.
1977. Organization and communication. *In* Wimsatt, W. (ed.), Biology of bats. Vol. 3, New York, Academic Press.

Buckland-Wright, J. C.
1978. Bone structure and patterns of force transmission in the cat skull (*Felis catus*). Jour. Morph., vol. 155, pp. 35–62.

Darwin, Charles
1859. On the origin of species by means of natural selection. London, J. Murry, 502 pp.

Elliot, D. G.
1904. The land and sea mammals of Middle America and West Indies. Field Columbian Mus. publ. no. 95, Zool. ser. 4, pt. 2, pp. i–xiii, 441–850.

Felten, H.
1956. Fledermause (Mammalia: Chiroptera) Aus El Salvador. Teil 3. Senckenbergiana Biologica, vol. 37, pp. 179–212.

Freeman, Patricia W.
1981. A multivariate study of the family Molossidae (Mammalia: Chiroptera) morphology, ecology, evolution. Fieldiana Zool., new ser., no. 7, publ. 1316, vii + 173 pp.

Grant, P. R.
1965. The adaptive significance of size trends in island birds. Evolution, vol. 19, pp. 355–367.

1972. Convergent and divergent character displacement. Biol. Jour. Linn. Soc., vol. 4, pp. 39–68.
1975. The classical case of character displacement. Evolutionary Biol., vol. 8, pp. 237–265.

Greenhall, A. M.
1959. The ecological role of Trinidad bats, especially the vampire and bat rabies. Vet. Record, no. 71, pp. 188–190.

Hahn, W. L.
1907. A review of the bats of the genus *Hemiderma.* Proc. U.S. Natl. Mus., no. 32, pp. 103–118.

Hall, E. R.
1981. The mammals of North America. Vol. II, New York, John Wiley & Sons, Inc., pp. v–vi, 601–1181, index 1–90.

Hall, E. R., and K. R. Kelson
1959. The mammals of North America. Vol. I, New York, Ronald Press Co., pp. i–xxx, 1–546, index 1–79.

Handley, C. O., Jr.
1966. Checklist of the mammals of Panama. *In* Wenzal, R. L., and V. J. Tipton et al. (eds.), Ectoparasites of Panama. Chicago, Field Museum of Natural History, pp. 753–795.

Heaney, L. R.
1978. Island area and body size of insular mammals: evidence from the tricolor squirrel (*Callosciurus prevosti*) of South East Asia. Evolution, vol. 32, pp. 29–44.

Heithaus, E. R., and T. H. Fleming
1978. Foraging movements of a frugivorous bat *Carollia perspicillata* (Phyllostomatidae). Ecol. Mon., vol. 48, pp. 127–143.

Hildebrand, Milton
1974. Analysis of vertebrate structure. New York, John Wiley & Sons, xv + 710 pp.

Johnson, R. F., and R. K. Selander
1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. Evolution, vol. 25, pp. 1–28.

Koopman, Karl F.
1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Amer. Mus. Novitates, no. 2651, pp. 1–33.

La Val, R. K.
1970. Banding returns and activity periods of some Costa Rican bats. South West Nat., vol. 15, pp. 1–10.

Leamy, L.
1983. Variance partitioning and effects of sex and age on morphometric traits in random breed house mice. Jour. Mammal., vol. 64(1), pp. 55–61.

Linnaeus, C.
1758. Systema naturae. Per regna tria naturae, secundum classes. (Reprint ed. of 1894–"Cura Societatis Zoologicae Germanicae iterum edita.") iii + 824 pp.

McNab, Brian K.
1971. On the ecological significance of Bergman's rule. Ecology, vol. 52(5), pp. 845–855.

Miller, G. S., Jr.
1924. List of North American Recent mammals. Bull. U.S. Natl. Mus., no. 128, pp. xvi–673.

Myers, Philip
1978. Sexual dimorphism of vespertilionid bats. Amer. Natur., vol. 112, pp. 701–711.

Nagorsen, D., and J. D. Tamsitt
1981. Systematics of *Anoura cultrata, A. brevirostrum* and *A. werckleae.* Jour. Mammal., vol. 62, pp. 82–102.

Nei, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent
1975. Statistical package for the social sciences (SPSS), 2nd ed. New York, McGraw Hill Book Co.

Patton, James L., and A. L. Gardner
1971. Parallel evolution of multiple sex-chromosome systems in phyllostomatid bats, *Carollia* and *Choerniscus.* Experientia, vol. 27, pp. 105–106.

Peterson, Randolf L.
1965. A review of the bats of the genus *Ametria,* family Phyllostomidae. Royal Ontario Mus., Life Science Contrib., no. 65, pp. 1–13.

Pine, Ronald H.
1972. The bats of the genus *Carollia.* Texas A & M Univ. Agr. Exp. Sta. Tech. Monogr., no. 8, pp. 1–125.

Porter, F. L.
1975. Aspects of social behavior in *Carollia.* Paper presented at Sixth Natl. Amer. Symp. on Bat Research, Las Vegas, Nevada.

Power, D. M., and J. R. Tamsitt
1973. Variation in *Phyllostomus discolor* (Chiroptera:Phyllostomatidae). Canadian Jour. Zool., vol. 51, pp. 245–276.

Ralls, K.
1976. Mammals in which females are larger than males. Quart. Rev. Biol., vol. 51, pp. 245–276.

Rees, J. W.
1970. A multivariate morphometric analysis of divergence in skull morphology among geographically contiguous and

isolated groups of White Tailed Deer (*Odocoileus virginianus*) in Michigan. Evolution, vol. 24, pp. 220–229.

Stock, A. D.
1975. Chromosome banding pattern homology and its phylogenetic implications in bat genera *Carollia* and *Choeroniscus*. Cytogen. Cell Gen., vol. 14, pp. 34–41.

Straney, Donald O.
1978. Variance partitioning and nongeographic variation. Jour. Mammal., vol. 59(1), pp. 11–21.
1980. Relationships of phyllostomatinae bats: Evaluation of phylogenetic hypothesis. Ph.D. dissertation, Univ. Calif., Berkeley. Dissertation abstr. B. Sci. Eng., 41(7):2519, Jan., pp. 1–278.
1983. Michigan State University, East Lansing, Michigan. Personal communication.

Straney, Donald O., M. H. Smith, I. R. Greenbaum, and R. J. Baker.
1979. Biochemical genetics. *In* Baker, R. J., J. Knox Jones, Jr., and Dilford C. Carter (eds.), Biology of bats of New World family Phyllostomatidae. Part III. Special Publ., The Museum, Texas Tech. Univ., pp. 157–176.

Wishart, David
1978. Clustan, cluster analysis package. Univ. College London, 19 Gordon St., London, WCIH OAH.